COSTS AND BENFITS OF GROUP LIVING IN AN UNUSUAL SOCIAL SPIDER, *DELENA CANCERIDES*

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by

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Virtually all spiders are predators, and many are cannibalistic. Of the handful of species that tolerate conspecifics and sustain long-term associations, nearly all spin a web or silken retreat. Previous research on these social spiders showed that many of the benefits they derive from group living depend on these silken structures. The social huntsman spider of Australia, *Delena cancerides*, is the exception and only lives under the bark of trees. I studied the costs and benefits of group living in this species, given that many of the benefits ascribed to other species are impossible without a web, in three contexts: (1) predator defense, (2) foraging, and (3) dispersal. I examined predator defense by introducing potential predators into field colonies that had been manipulated to allow observations and into captive colonies in the laboratory. The single adult female of the colony was the primary defender of the colony, while younger spiders were ineffective at repelling predators. I examined foraging by observing natural prey capture in the field, introducing prey into field colonies, and recording the condition of field spiders at the time of collection**.** Spiders predominantly foraged individually; however, some prey captured inside the retreat was shared, and younger

spiders benefited from sharing prey captured by their older siblings. I examined dispersal into neighboring colonies through a combination of allozyme analyses and direct observations in the field and laboratory. Young spiders can and do immigrate into foreign colonies; however, older spiders were usually attacked in foreign colonies, and thus their dispersal options are constrained. Through the use of nest boxes, I showed that competition for a new bark retreat is intense and that spiders should wait in their natal retreat until they are larger and better competitors for a new retreat. Together, these data show that the bark retreat is indeed critical to the social biology of *D. cancerides*. Without the web some forms of cooperation found in other social spiders never evolved, yet the reliance on a rare bark retreat also promotes group cohesion, as is found in many social vertebrates.

BIOGRAPHICAL SKETCH

In May of 2005, Eric C. Yip graduated with a B.S. in Ecology and Evolutionary Biology from the University of Arizona, summa cum laude and with honors. His honors thesis on the relationship between colony size and foraging success in the social spider, *Anelosimus eximius*, sparked his interest in the evolution of social behavior in spiders and would eventually be published in The Proceedings of the National Academy of Sciences, USA. He chose to continue his work on social spiders with Dr. Linda S. Rayor at Cornell University's Department of Entomology. From 2005 to 2012, he has studied the costs and benefits of group living in the unusual social spider, *Delena cancerides*. Eric is grateful to the Fulbright Fellowship, the National Science Foundation's Graduate Research Fellowship, Cornell University's Sage Fellowship and Liu Memorial Fund, in addition to smaller awards, that have funded his research. These grants have allowed him to spend three years conducting field work in Australia as a visiting fellow at The Australian National University. He has presented his work at meeting by the American Arachnological Society, the International Arachnology Congress, the International Society for Behavioral Ecology, and the Animal Behavior Society. He was awarded second place Best Student Oral Presentation at two International Arachnology Congresses in 2007 and 2010. He was also selected to compete in the Animal Behavior Society's Allee Competition in 2012. He has been awarded the Blaustein Fellowship and the Kreitman Fellowship to conduct post-doctoral work at Ben-Gurion University of the Negev with Dr. Yael Lubin.

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TABLE OF CONTENTS

CHAPTER 1

Aliens among us: Nestmate recognition in the social huntsman spider, *Delena cancerides*

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Abstract. Unlike all other social spiders, the social huntsman spider, *Delena cancerides* has been reported to rapidly respond to non-nestmates with lethal aggression, similar to the behavior of some eusocial insects. We tested for the presence of nestmate recognition in *D. cancerides* under laboratory conditions by introducing 105 unrelated alien conspecifics into foreign colonies and comparing their behavior to 60 control spiders removed and returned to their natal colony. Spiders demonstrated nestmate recognition by investigating alien spiders far more than nestmates and by resting closer to nestmates than to aliens. Serious attacks or deaths occurred in 23% of all trials; however, aggression was not directed significantly more toward aliens than to nestmates. Most notably, aggression was largely mediated by the adult females (resident or alien), who were most likely to attack or kill other subadult or mature individuals. Young individuals (resident or alien) were largely immune from serious aggression. Spiders recently collected from the field tended to be more

aggressive than spiders born and raised in the laboratory, possibly due to blurring of recognition cues related to laboratory husbandry. Our findings support the prediction that nestmate recognition should evolve when there is a benefit to discriminating against non-kin, as in this social spider system where foraging individuals may enter a foreign colony and the colony retreat is a limited resource.

Key words: Social spiders, Nestmate recognition, aggression

Introduction

The ability to discriminate kin from other conspecifics is a common trait among social animals, as it allows altruistic behaviors to be preferentially directed toward kin (Hamilton 1964; Hölldobler & Wilson 1990; Holmes 2004). Most eusocial insects recognize their nestmates, with the resolution of kin discrimination at the level of the colony (Breed et al. 1994; Clément & Bagnères 1998; Strassmann et al. 2000; Tarpy et al. 2004). While nestmate recognition is common among the eusocial insects (Wilson 1971; Singer & Espelie 1992; Clément & Bagnères 1998; Vander Meer & Morel 1998) nestmate recognition is rare or absent in the subsocial and social arachnids (Lubin & Bilde 2007).

There is a continuum of social behavior in the spiders from small subsocial mother-offspring-sibling groups to complex, cooperative societies of thousands of individuals (Buskirk 1981; Avilés 1997; Lubin & Bilde 2007). Most social spiders, despite multiple evolutionary origins, share a suite of traits that includes the acceptance of alien spiders (unrelated and unfamiliar conspecifics) into the group without overt

aggression (Lubin & Bilde 2007). These social spider species do not appear to differentiate between conspecific aliens and members of their own colony (Pasquet et al. 1997), silk from kin or non-kin (Bilde et al. 2002; Buser 2002), or even heterospecific from conspecific spiders in the same genus (Seibt & Wickler 1988a).

Most social spiders may have never evolved nestmate recognition because the costs of sharing resources are relatively small, and non-relatives are encountered only rarely. While there is undoubtedly competition for resources within social spider colonies (Ward 1986; Seibt & Wickler 1988b; Avilés & Tufiño 1998; Bilde et al. 2007), the benefits of group-living may mitigate the costs of sharing resources (Rypstra 1989; Avilés 1997; Uetz & Hieber 1997; Avilés & Tufiño 1998; Jones & Parker 2002; Whitehouse & Lubin 2005). Migration among colonies is rare in most cooperative spiders, and in a number of species, extreme inbreeding is the norm, suggesting that these spiders encounter aliens rarely (Avilés 1997; Lubin & Bilde 2007).

Of the social spiders, only the Australian huntsman spider, *Delena cancerides* Walckenaer (Sparassidae), has been reported to rapidly attack alien conspecifics (Rowell & Avilés 1995; Beavis et al. 2007). When aliens were introduced into laboratory colonies, colony members killed and partially ate aliens, typically within 24 h (Rowell & Avilés 1995). In addition to aggression among adult females, both adult males and juveniles (all juveniles were unsexed) were killed, and both adults and juveniles killed aliens. However, preliminary experiments by L. Rayor indicated that adult males and small juveniles were usually accepted into the colony, while most aggression was directed toward reproductive or subadult females. A recent study on kin-recognition in *D. cancerides* supports these preliminary results, showing that adult females usually

accept non-kin juveniles if they are small enough but kill older juveniles (Beavis et al. 2007). While the extent of the aggression toward non-kin seen in *D. cancerides* appears to be unique among the social spiders, preferential cannibalism of non-kin has been demonstrated in a few other spider species. Spiders preferentially cannibalize non-kin after several days or weeks of starvation in two subsocial species (Evans 1999; Bilde & Lubin 2001) or shortly after mother and offspring disassociate in two species of solitary wolf spiders (Anthony 2003; Roberts et al. 2003).

The ecology of *D. cancerides* differs dramatically from other social spiders and is predicted to favor the evolution of nestmate recognition. *Delena* is one of only two social spider genera with spiders that do not live in connected or communal webs (Evans 1995; Rowell & Avilés 1995; Avilés 1997). Spiders of the other non-web building social spider genus, *Diaea*, construct expandable retreats of leaves and silk (Evans 1995). In contrast, *D. cancerides* spiders live exclusively under tree bark. Whereas the acceptance of immigrants into a web-based spider colony may increase the colony's total web area and prey capture capacity, the relatively small *Delena* retreats cannot be created or expanded by the spiders (Rayor et al. in prep.). Benefits associated with living under the retreat (protection from abiotic elements, defense from predators, prey sharing by younger animals, etc.) are unlikely to increase with the addition of immigrants. Moreover, as only a single adult female typically reproduces per colony, older immigrant females are potential reproductive competitors of the breeding female or her daughters. In suitable habitats, *D. cancerides* colonies may be as close as 1 m apart, and some single trees house multiple distinct colonies (Rayor et al. in prep.). Unlike all other web-based social spiders, these spiders are central place

foragers, leaving the retreat at night and returning at dawn. Spiders move as far as 10 m on foraging bouts (Yip & Rayor see Chapter 2). It is therefore highly probable that conspecific aliens are encountered in the field. If accepting immigrants into the colony imposes a potential cost to the residents – or some portion of them - we predict that individual *D. cancerides* spiders will discriminate between nestmates and aliens.

To test the prediction that members of *D. cancerides* colonies discriminate nestmates from alien conspecifics, we introduced individuals of different ages and sexes into foreign colonies in the laboratory. The explicit behaviors indicative of nestmate recognition are difficult to characterize. The reactions of eusocial insects to alien intruders range from accepting the alien while partially withholding food resources, to frequent investigative touches, to outright attack (Wilson 1971; Hölldobler & Wilson 1990; Pearce et al. 1990). Other eusocial insects apparently lack colony level recognition (Clément & Bagnères 1998; van Wilgenburg et al. 2007). In light of these highly variable responses, we evaluated both overt aggression and more subtle behaviors that may differ between nestmates and aliens. We compared interactions with aliens to those with nestmates, taking any differences in behavior to be indicative of nestmate recognition. Finally, we examined how the age and sex of the alien and characteristics of the host colony correlate with the probability of aggression.

Materials and Methods

Study organism and care

Delena cancerides is endemic to southern Australia and Tasmania (Main 1962). Spiders form colonies of up to 300 individuals under the bark of *Acacia*, *Eucalyptus*,

Callitris and *Casuarina* trees (Rowell & Avilés 1995; Rayor et al. in prep.). Most colonies consist of a single adult female with multiple cohorts of immature offspring living together although colonies with 2-3 adult females are occasionally found in the field (Rayor et al. in prep.). Only a single female successfully produces egg sacs at a time within a colony (unpubl. data). Spiders live for ~2.5 years and typically reach sexual maturity in 10 or 11 instars. We considered the large-bodied seventh through ninth instars whose sexes can be readily distinguished to be subadults. Colonies were collected from 10 sites in southern Australia (2 in the Australian Capital Territory, 6 in New South Wales, 1 in South Australia, and 1 in Victoria). While chromosomal arrangements may differ considerably among *D. cancerides* populations from different areas in Australia, all interbreeding, morphological, and molecular evidence indicates that these spiders remain a single species (Sharpe & Rowell 2007).

Colonies used in this study consisted of either third or fourth generation descendants of spiders collected from the field in January – March 2002 (here termed 'laboratory' colonies), or spiders recently collected, either in January-March 2002 for trials conducted in 2002 or February-April 2006 for trials conducted in 2006 (here termed 'wild' colonies). Spiders were housed in glass terraria with total surface areas of 2743 or 4888 cm^2. To replicate their retreats under tree bark, clear 3mm thick Plexiglas sheets were attached 1–2 cm away from the long sides of the terraria with layered squares of Velcro, creating thigmotactically appealing retreats of 504 or 888 cm^2 that are consistent with retreat sizes found in the field (Rayor et al. in prep.). Colonies with more and/or larger individuals were housed in larger terraria. Substrate at the bottom of the terraria was a mixture of soil and vermiculite. Each colony had a shallow water dish.

Colonies were maintained at room temperature (22-26º C) and approximately 12 h light and dark cycles prior to introduction trials; during the first day of trials, colonies were exposed to constant light so that experimental spiders could be easily identified on film. *Delena cancerides* is nocturnal in the wild, yet spiders in the laboratory exhibit the same behavioral repertoire in the light as they do in the dark (e.g. feeding, mating, laying eggs, and all behaviors quantified in this study, unpubl. data). Colonies were fed 1 cricket (*Acheta domesticus*) or housefly (*Musca domestica)* per spider 1-2 times per week prior to introductions and again immediately preceding an introduction trial to standardize hunger levels.

Introduction Experiments

We define 'aliens' as conspecific spiders introduced to the terraria of unfamiliar, unrelated colonies. 'Controls' refer to colony nestmates or kin, of the same age (within one instar) and sex as the alien, which were removed and returned to their natal colony during introduction experiments. The effects of familiarity and kinship are confounded in this study; however, the distinction between the two is mechanistic, with kinship being a form of 'allele recognition' or 'phenotype matching' and familiarity being recognition by 'prior association' (Holmes 2004; Mateo 2004). In this study, we were not concerned with the mechanisms maintaining nestmate recognition, but rather the characterization of behaviors that might indicate the presence of nestmate recognition. We report 15 experimental trials in 2002 and 90 experimental trials in 2005/2006.

In 11 of the 15 2002 trials, only alien spiders, third instar to subadult females, were introduced into foreign colonies composed of an adult female and one or two cohorts of young. In the remaining 4 trials, an adult female, a subadult female, an adult

male and a subadult male were paired with a nestmate of the same age and sex that had been removed from its natal colony 1-2 months prior. Each pair of spiders was introduced into a colony that had a resident adult female. Spiders were placed in vials that were then opened inside terraria, and the spiders moved out of the vials of their own volition. Survivorship was tracked for 1 week, but all deaths occurred within 24 hr. Survivorship data for the 2002 trials were qualitatively similar to those for the 2005/2006 trials, in terms of the frequency of attack and the age of spiders attacked. Therefore, these data were added to our analyses; however, because paired nestmates were separated from their natal colony for long periods of time, these data are not included in our comparisons between aliens and controls.

We conducted 90 experimental introductions from September 2005 to July 2006. Colonies were classified as either wild or laboratory colonies, and as having an adult female ('AF colonies') or lacking an adult female ('no-AF colonies'). The origin of the colony (laboratory or wild) determined the classification of the trial. Aliens were classified as adult females, adult males, or immature spiders (unsexed juveniles third - sixth instar or sexed subadults seventh-ninth instar), and assigned an instar (age) based on body size (see Table 1). Aliens were paired with controls in 60 trials; no controls were used in 30 trials because colonies in these trials did not contain a nestmate of similar age and the same sex as the alien.

Experimental trials in 2005/2006 followed the following protocol: We lightly sedated alien and control spiders with CO_2 and weighed them on a Mettler Toledo scale (AG285). For each spider, we used Spi 2000 calipers to measure the maximal width of the cephalothorax and length of the second leg (the longest leg), from the tip of the

tarsus to the coxa. Using a toothpick, Testors enamel paint was applied to the ventral and dorsal surfaces of the cephalothorax, taking care to leave the eyes, mouthparts, and book lungs unobstructed. Once the experimental spiders were fully recovered from the effects of the CO_2, they were simultaneously and gently coaxed onto the Plexiglas retreats. In all, the measuring and marking process took 15 min or less. An effort was made to minimize disturbance to the colony as experimental animals were introduced. We directly observed and recorded behavior for the first hour. Thereafter, terraria were videotaped for 15 h on a 30 s interval, using one of two types of Sony digital video cameras (DCR-TRV900, DCR TRV30), to track behavior and survival of the experimental spiders. While the 30 s interval recording undoubtedly missed some short interactions, more intense confrontations, including killing and/or cannibalism take longer than 30 s, ensuring that these major events were recorded. For 3 days following the initial introduction, we measured nearest neighbor distance and survival for the control and alien once a day at approximately 24 h intervals.

We recorded behavior defined by the *Delena cancerides* ethogram previously developed by L. Rayor and R. Walsh (unpubl. data). We recorded both of the experimental spiders' initial reactions in the first 5-10 s of the trial as calm (no movement or slow walking) or as frantic (erratic running). Throughout the study we recorded three primary types of contact: 'face-offs' where spiders face each other with first and second legs touching the other and often circle around one another with legs entwined and bodies held at a distance (note: face-offs occasionally preceded an attack by one participant on the other), 'touches' where spiders rapidly touch or tap any part of

another spider's body, and 'aggregation' where spiders sit in contact with others for > 1 min.

Colony demographics varied naturally, but to minimize colony disruption, we made no attempt to standardize spider density. Because alien and control spiders were introduced into the same colony simultaneously, spider density cannot account for differences in responses between aliens and controls. However, spider density was considered as a factor in explaining overall patterns of aggression.

Analyses

Because the number of colonies with suitable age-groups was limited, 26 of a total of 59 colonies were used more than once, depending on the age range of the spiders. No colony was used more than 5 times. However, to make trials as independent as possible, no spider was ever used twice as an alien. We further use colony as a random effect where possible.

We compared continuous responses (contacts and nearest neighbor distances) between aliens and controls using Wilcoxon signed rank tests because our data were not normally distributed. Binomial responses (aggression, initial reactions, whether spiders rested in contact) by aliens and controls were compared using a generalized linear model (GLM) with a binomial distribution. To account for the pairing of alien and control spiders within trials and subsequent correlation among data, the standard errors were corrected by a generalized estimator equation (GEE) with the trial as the repeated subject. Nestmate status (alien or control) was the explanatory variable. Sex, age, and their interactions with nestmate status, in addition to collection region, spider density, the status of the colony as wild or laboratory, and whether the alien was from the same

collection region or a different collection region as the residents were also included in the models as possible variables of interest. These parameters were removed from the model if they failed to explain a significant portion of the variance.

We used mixed models, with colony as a random effect, to examine the relationships between nearest neighbor distance and sex and age. We used contingency tables and likelihood ratio tests to examine the correlations between the colony characteristics (laboratory or wild; with or without an adult female; type of alien) and aggression. Not all trials yielded results for all measures, so separate sample size is reported for all analyses. SAS was used for GLM and GEE analyses. All others were conducted with JMP.

Results

Aggression

Out of all 105 trials from all years, 24 (23%) resulted in either the alien or control experiencing aggression. Most aggression was mediated by adult females. Of 24 trials with aggression, 18 (75%) involved adult females as aggressors, and an additional two involved subadult (eighth instar) females.

Of the 11 alien-only introductions in 2002, three spiders (27.3%; a sixth instar and two subadult females) were killed within 24 hr. All aliens fifth instar and younger survived introductions, as well as two seventh instar females. All but one alien that survived rested with colony members after one day; the other alien rested with the group after two days. In the four paired kin and non-kin trials of 2002, all kin survived.

However, the alien adult female was attacked and injured, while the subadult female, subadult male, and adult male survived without major incident.

Of all 90 trials (both paired with controls and unpaired) done in 2005 and 2006, 3 trials resulted in missing and presumed eaten nestmate spiders that could not be attributed to a specific aggressor (See Table 1). Of the remaining 87 trials, 19 (22%) resulted in either the alien being killed or attacked (n = 11 trials) or the alien killing or attacking a colony member (n = 8). Ten of 60 paired trials (17%) resulted in the control being attacked or attacking another individual. In 6 of these 10 trials, aggression occurred between the two introduced animals, not another member of the colony. When aggression occurred between adult female aliens and their paired adult female control, it was difficult to distinguish whether the aggression indicated the exclusion of a non-nestmate or competition among adult females to secure the retreat as a breeding site, as there usually is only one adult female per colony. To be conservative, in these cases both the alien and control were designated as experiencing aggression. GLM analysis correcting for paired aliens and controls within trials by GEE, showed that aggression was not more directed toward aliens than controls (n = 136; alien/control: $z = 0.92$, $p = 0.36$) but that older spiders experienced increased aggression (age: $z = 2.45$, $p = 0.014$), as did spiders in wild colonies (laboratory/wild: $z = 3.09$, $p = 0.005$). Higher spider density increased the rates of aggression (spider density: $z = 2.78$, $p = 0.002$). Other parameters were not significantly related to the occurrence of aggression, including introduced spiders' sex, collection region, or whether the alien was from the same collection region or a different collection region from the residents.

Initial reactions

Aliens tended to behave more frantically than controls in the initial 5-10 s of each introduction trial. Of 82 aliens introduced, 34 (41%) had an initial frantic reaction while only 14 of 55 controls (25%) did. Both age and nestmate status (alien or control) approached significance when considered together (GLM corrected by GEE: n = 138; alien/control: $z = 1.91$, $p = 0.057$; age: $z = 1.78$, $p = 0.075$). Nestmate status became significant if age was removed from the model (GLM corrected by GEE: n = 138; alien/control: $z = 1.99$ $p = 0.046$).

Contacts

Introduced spiders engaged in three major forms of contact (touch, face-off, and aggregation) with colony members. In 60 trials, aliens and controls differed depending on whether contact was received or initiated by the introduced spider (Figure 1). When all three forms of contact were summed, aliens were subjected to significantly more contact than controls (Wilcoxon signed rank test: $T = -226.5$, $p = 0.018$), and most of this difference was from contact received as opposed to contact initiated (contact received: $T = -232$, $p = 0.007$; contact initiated: $T = -90$, $p = 0.36$). This effect was driven largely by a difference in touches received by aliens ($T = -195.5$, $p = 0.012$). Aggregation received and face-offs received were also greater for aliens than controls, but the differences were not significant (aggregation: $T = -17$, $p = 0.09$; face-off: $T = -1.5$, $p = 0.5$). No measure of initiated contact differed between aliens and controls (touch: $T = -90.5$, $p = 0.309$; aggregation: $T = -25$, $p = 0.27$; face-off: $T = -1.5$, $p = 1.0$). However, aliens tended to aggregate (spiders remained in relatively inactive contact for > 1 min) more than controls during the first hour regardless of which spider initiated the contact ($T = -43$, $p = 0.020$).

Nearest neighbor distance

The effect of increased aggregation by aliens did not persist beyond the first hour. Over the 3 subsequent days (distance measured once per day), controls averaged only 6.1 cm away from their nearest neighbor, compared to 7.7 cm for aliens ($T = -121.5$, $n = 42$, $p = 0.028$). Average nearest neighbor distance, for both aliens and controls, significantly increased with age but showed no relationship with respect to sex. (Using a mixed model with age and sex as variables, colony as a random effect, and with colony origin (laboratory/wild) and nestmate status (alien/control) as covariates: adjusted $R^2 = 0.53$, $n = 80$; ln(age); $F = 11.0$, $p = 0.0014$; no significant interactions: ln(age)*alien/control $F = 2.89$, $p = 0.094$; ln(age)*laboratory/wild $F = 0.60$, $p = 0.44$; sex $F= 0.78$, $p = 0.38$; no significant interactions: sex*alien/control $F = 0.55$, $p = 0.46$; sex*laboratory/wild $F = 0.50$, $p = 0.48$). Controls were more likely to rest in direct contact with other spiders than were aliens during the initial 3 days, as were younger spiders (GLM corrected by GEE: $n = 110$; alien/control: $z = 2.69$; $p = 0.007$; age: $z = 3.76$, $p = 0.0002$).

Wild versus laboratory reared spiders

As indicated by the aggression analysis, spiders from colonies that had recently been captured in the wild were significantly more aggressive than individuals born and raised in the laboratory (Table 2). Adult females introduced into wild colonies were more likely to experience aggression than those introduced into laboratory colonies, either by fighting with the resident adult female or by attacking and sometimes consuming juveniles if a resident adult female was absent. Males tended to be attacked more in wild than laboratory colonies, but this was not significant with a Bonferroni correction.

Immature spiders experienced similar aggression when introduced into both wild and laboratory colonies. Control spiders experienced similar aggression levels regardless of whether they were from wild or laboratory colonies. However, there was a non-significant trend for adult female controls to experience more aggression if they were from wild colonies (Table 2). This trend was due to the control adult female attacking the alien, rather than from conflict between the control and the rest of the colony.

Discussion

Do Delena cancerides *spiders recognize nestmates?*

Our results support the hypothesis of nestmate recognition in *D. cancerides*. Spiders were able to differentiate alien from control and showed increased investigative contact toward alien spiders. Increased contact toward unfamiliar animals has been found in a variety of taxa, including ground squirrels (Mateo 2002), voles (Fadao et al. 2000), and ants (Dahbi & Lenoir 1998). The reason for this pattern may be that unfamiliar recognition cues take longer to process and match to a 'template' (Mateo 2004). Alien spiders also rested farther away from colony member than controls on average, reflecting an absence of integration into the colony.

We detected a marginally significant difference in initial reactions (frantic running or calm) between aliens and controls. Our behavioral assay is likely to be conservative in indicating stress caused by relocation into an unfamiliar colony. While frantic running clearly demonstrates heightened excitement, resting perfectly still may reduce the probability of attracting the attention of a hostile adult female. Thus, some outwardly

calm spiders may have been stressed. Nevertheless, this result is consistent with our other results showing spiders can differentiate aliens from nestmates.

Aggression comparisons

In contrast, we found little evidence that aggression is primarily directed toward aliens. Aliens were not subjected to more aggression than controls, and an individual's age strongly influenced the probability of aggression. Because aggression was most common among adults, particularly adult females, aggression may be more strongly influenced by a spider's reproductive status than by its nestmate status. Adult females may be eliminating other adult and subadult females that might usurp the retreat and breed regardless of kinship, rather than excluding aliens from a limited resource. Our data, however, cannot distinguish between these two hypotheses. In either case, the prevalence of aggression among adult females suggests that there must be some cost for multiple adult females to cohabit within a single retreat.

In our studies, aggression levels were relatively low (in 23% of trials) compared to the extreme aggression originally reported by Rowell and Avilés (1995). Rowell and Avilés (1995) included data from 12 introductions, 11 of which were with unrelated spiders. Ten of these 11 introductions resulted in the death of the alien or in the alien killing colony members. Rowell and Avilés (1995) also reported three instances when juveniles or subadults attacked or killed other spiders. While immature spiders were present in most trials, we recorded only two trials with attacks by subadults or juveniles. Part of this discrepancy is related to differences in experimental conditions, as our introductions were done with as little disturbance as possible to the introduced animals or resident colony. Colonies in our study were provided with acceptable retreats and

were well fed in comparison to those in the earlier study (D. Rowell, pers. com.). Another reason may be the decreased aggression seen in the laboratory raised spiders used in this study.

Our results are more consistent with those of Beavis et al. (2007), who found that in 11 of 34 trials *D. cancerides* juveniles cannibalized non-kin (all did so within 24 h). In the remaining trials, spiders starved before cannibalizing kin or non-kin (Beavis et al. 2007). Our finding that older spiders are more likely to experience aggression was also consistent with the Beavis et al. (2007) study, which showed that females did not attack alien juveniles unless they reached a certain size (a carapace width in excess of 6 mm, which is equivalent to the seventh instar, our unpubl. data). While Beavis et al. (2007) confirm our results that most *D. cancerides* refrain from aggression against aliens, their rates of aggression by juveniles are still much greater than suggested by the two instances of aggression by juveniles or subadults reported here. The discrepancy may be again due to differences in husbandry as their animals were housed in very small containers, and our results show that high spider density promotes aggression. Our inability to detect aggression preferentially directed toward aliens may therefore have two causes: One, the rarity of aggression by immature spiders effectively limited the opportunity to observe such preferential aggression. Two, most aggression was between adult females, and we could not determine whether this aggression was due to the elimination of aliens or reproductive competitors.

Our rate of aggression is also low compared to Evens (1999) and Bilde and Lubin (2001), who also examined preferential cannibalism of non-kin spiders in a social context, though direct comparisons cannot be made because we did not starve our

spiders or record aggression weeks after introduction. Instead we were concerned with short-term reactions and the exclusion of aliens from the retreat by well fed animals. Our aggression rates might be considerably higher had we included trials with starved spiders.

Spiders in wild colonies were strikingly more aggressive than those in laboratory colonies. This difference may be due to laboratory conditions that blur nestmate recognition cues. Spiders from colonies in the field live under the bark of different tree species in different habitats, eat a wide variety of arthropod prey, and each retreat has been used for a variable number of generations resulting in a build up of prey remains at the base of the colony. In contrast, animals raised in the lab are housed in similar glass terraria and given the same substrate and food. Numerous studies have shown that the recognition cues of social insects are partly derived from the nest, and standardized nest material may make recognition more difficult (Obin 1986; Singer & Espelie 1992; Breed et al. 1995; but see Ross & Gamboa 1981). If all spiders, regardless of colony, share nest-derived recognition cues, perhaps spiders face greater uncertainty (a greater overlap between alien and colony member cues) that would temper their interactions. Laboratory conditions may also disrupt aspects of the spiders' life cycle that regulate aggression. For example, aggression could be dispersal mediated, so that spiders that are unable to disperse reduce aggression to avoid killing siblings. In the laboratory, spiders were given few dispersal opportunities. The higher levels of aggression in wild animals indicate that spiders in the field are likely to behave more aggressively than reported here. However, because spiders live under bark, detailed behavioral observations in the field have been difficult. Fully describing the role

of nestmate recognition in intercolony contacts in *D. cancerides* awaits rigorous field studies, through the use of nest boxes or other manipulations of the retreat to allow non-intrusive observations.

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Alien introduced	Presence of adult female	Years					
		2002		2005/2006			
		Wild		Laboratory		Wild	
		Alien only	Alien + Kin	Alien only	Alien + Control	Alien only	Alien + Control
Adult female	AF	0	1	0	10	0	4
Adult female	No-AF	0	0	3*	3	5*	2*
Immature	AF	11	2	9	9	0	7
Immature	No-AF	0	0	5	13	0	5
Adult male	AF	0	1	5	5	3	2
Total		11	4	22	40	8	20

Table 1: Sample size for introductions with different ages and sexes of spiders. AF indicates the presence of a resident adult female in the colony; No-AF indicates the absence of a resident adult female. * One trial in each of these three categories involved the disappearance of spiders from the colony, and no aggressor could be identified. These trials are not included in aggression comparisons but are still included in all other measures.

Introduced Spider	Spider/female presence	Lab or Wild	% Aggression	χ^2 (df)	N	p-value
Aliens	Female/AF	Lab Wild	30.00 100.00	8.51 (1)	10 5	0.0035*
	Female/No-AF	Lab Wild	0.00 80.00	8.46 (1)	5 5	0.0036*
	Immature/AF	Lab Wild	11.11 19.05	0.57 (1)	18 20	0.45
	Immature/No-AF	Lab Wild	11.11 0.00	1.03 (1)	18 5	0.31
	Male/AF	Lab Wild	0.00 50.00	7.013 (1)	10 6	0.0076
Controls	Female/AF	Lab Wild	30.00 80.00	3.51 (1)	10 5	0.061
	Female/No-AF†	Lab Wild	0.00 0.00	0.00 (1)	3 1	--
	Immature/AF	Lab Wild	0.00 0.00	0.00 (1)	9 9	--
	Immature/No-AF	Lab Wild	7.69 20.00	0.50 (1)	13 5	0.48
	Male/AF	Lab Wild	0.00 33.33	2.21 (1)	5 3	0.14

Table 2: The percentage of encounters involving aggression in laboratory ('lab') and wild spiders for each type of introduction. Spider/female presence designates the age and sex of spider introduced, adult female ('Female'), immature, or an adult male ('Male') and the presence ('AF') or absence ('No-AF') of a resident adult female in the colony. * indicates significance, accounting a Bonferroni correction, yielding a maximum p-value threshold of 0.00625 to achieve an α of 0.05 for the combined 8 tests. †While there was no adult female to use as a control in trials where the resident colony lacked an adult female, in 4 trials a large penultimate female was used as a control instead.

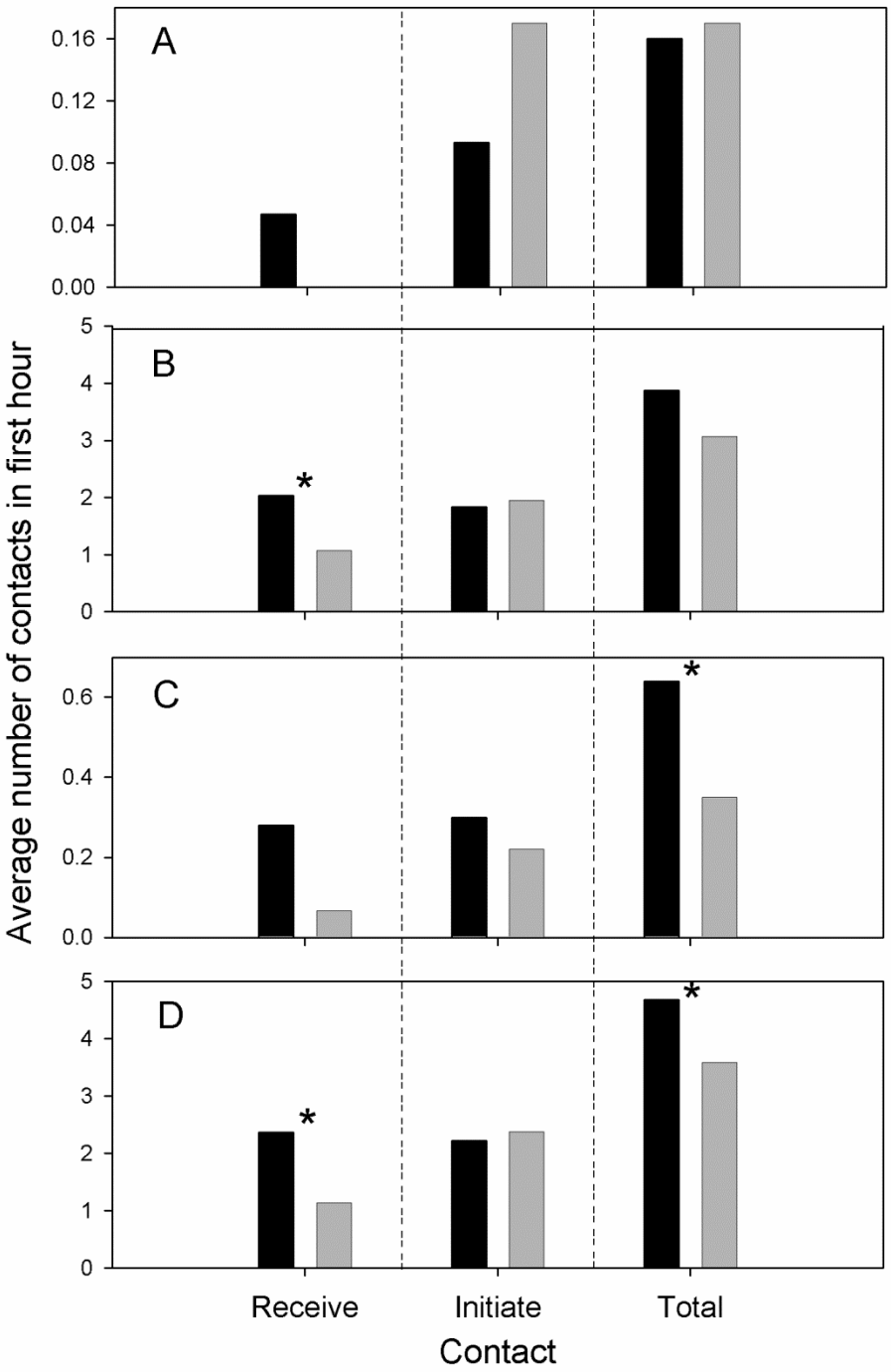

Figure 1. The average number of contacts received, initiated, and in total for aliens in black and for control spiders in gray. Contact is subdivided into A) face-offs, B) touches, C) aggregations, and D) total summed contact. *Asterisk* denotes significance.

CHAPTER 2

Do social spiders cooperate in predator defense and foraging without a web?

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Abstract. Nearly all social spiders spin prey-capture webs, and many of the benefits proposed for sociality in spiders, such as cooperative prey capture and reduced silk costs, appear to depend on a mutually shared web. The social huntsman spider, *Delena cancerides* (Sparassidae), forms colonies under bark with no capture web, yet these spiders remain in tightly associated, long-lasting groups. To investigate how the absence of the web may or may not constrain social evolution in spiders, we observed *D. cancerides* colonies in the field and laboratory for possible cooperative foraging and defense benefits. We observed spiders' responses to three types of potential predators and to prey that were introduced into retreats. We recorded all natural prey capture over 447 h both inside and outside the retreats of field colonies. The colony's sole adult female was the primary defender of the colony and captured most prey introduced into the retreat. She shared prey with younger juveniles about half the time but never with older subadults. Spiders of all ages individually captured and consumed the vast majority of prey outside the retreat. Young spiders benefited directly from maternal defense and prey sharing in the retreat. However, active

cooperation was rare, and older spiders gained no foraging benefit by remaining in their natal colony. *Delena cancerides* does not share many of the benefits of group living described in other web-building social spiders. We discuss other reasons why this species has evolved group living.

Keywords: Cooperation, sociality, spiders, foraging, predator defense, group living, constraints

Introduction

Sociality, including group living more generally, is a continuing conundrum in evolutionary biology (Alexander 1974; Krause & Ruxton 2002; Frank 2003). Group living carries with it automatic costs, such as increased competition and parasite transmission, and so organisms must derive substantial benefits from group living for it to evolve (Alexander 1974). As constraints are an inescapable feature of evolution (Gould 1980), whether sufficient benefits accrue for sociality to evolve and the nature of these benefits depend partly on the evolutionary history of the organism on which selection is acting.

Sociality is particularly rare in the spiders, suggesting that one or more features of their biology might limit social evolution. Here, we define 'social' broadly to encompass any species in which individuals form long-term associations, including colonial species (e.g. the Araneid orb weaver *Metepeira incrassata*) and species without alloparental care (e.g. the thomisid crab spider *Diaea ergandros*). All spiders are born grouped in both space and time within the egg sac, yet despite this, in over 99% of the 42,000+ identified spider species, individuals soon disperse to live solitarily (Avilés 1997; Whitehouse & Lubin 2005; Lubin & Bilde 2007; Platnick

2011). One reason that sociality is rare in the spiders may be that a prey-capture web is a critical preadaptation to spider sociality (Avilés 1997), and non-web building species comprise over half of all spiders (Blackledge et al. 2009). Most social spider species spin capture webs (Shear 1970), including species in families that do not typically build webs, such as the Lycosidae and the Oxyopidae (Brach 1976, Avilés 1994).

A survey of the literature on the benefits of group living proposed for spiders indicates that most benefits are contingent on a mutually shared web. Cooperative prey capture allows spiders to subdue prey that would otherwise be far too large for an individual spider (Buskirk 1981; Ward 1986; Jones & Parker 2002; Yip et al. 2008) and may even increase per capita food intake (Yip et al. 2008). Web vibrations caused by the prey struggling in the web act to simultaneously recruit multiple spiders (Burgess 1976), and additional web vibrations by other spiders facilitates hunting coordination (Krafft & Pasquet 1991). Thus, the web is crucial to cooperative prey capture in most of the social spiders. Even in the colonial spiders that do not cooperatively capture prey, orb weaving spiders may benefit from increased prey capture success through the ricochet effect, by which insects become easier to capture after they have rebounded off an adjacent spider's web (Uetz 1989). Similarly, webs are closely associated with antipredator defense in the social spiders. Spiders in groups may be better defended from predators, either by early warnings communicated through the web (Hodge & Uetz 1992) or by silk that hinders predators from penetrating into the core of colonies (Rayor & Uetz 1990; Evans 1998; Henschel 1998). Finally, spiders benefit from cooperative web construction and reduced individual silk costs (Avilés 1997; Lubin & Bilde 2007).

Like all Sparassidae, the social huntsman spider, *Delena cancerides* Walckenaer, does not construct a web, making it one of only two known genera of social spiders that does not build capture webs (Rowell & Avilés 1995; Evans 1995). Instead, these spiders live exclusively in retreats under tree bark (Rowell & Avilés 1995). Colonies usually consist of a single female and her offspring, which may consist of up to 5 intermingled cohorts that range in age from newly emerged young to penultimate subadults (Rayor et al. in prep.). Bark retreats appear to be occupied for successive generations. Based on laboratory observations and collection data, this species does not form societies with multiple breeding females. However, offspring remain together with their mother and siblings until sexual maturity, and spiders require about 1 year to mature (pers. obs.). Therefore, spiders in these long-term societies should be subject to the inherent costs associated with any long-term group. Allozyme analyses have shown that most offspring are full or half siblings, though unrelated migrants have been detected in about half of collected colonies (Yip et al. see Chapter 3). Spiders may, therefore, derive both direct and indirect benefits from group living that outweigh its associated costs. Without a capture web, however, many of the benefits of group living ascribed to other social spiders might not apply to this species.

The other spider genus with social species that lacks capture webs is *Diaea* (Thomisidae). Main (1988) and Evans (1998) studied the benefits of group living in *Diaea socialis* and *Diaea ergandros*, respectively, both of which form expandable retreats of silk and leaves. Evans (1998) found that while *Di. ergandros* spiders did not cooperate in defense against predators, they benefited from the barrier provided by their silk nest, which became larger and more protective as colony size increased. Sharing prey captured by the mother provided a considerable benefit to juveniles

(Evans 1998). Spiders usually foraged individually near retreat entrances (Main 1988).

Here, we examine the benefits *D. cancerides* spiders derive from group living to answer two questions: (1) Has evolution circumvented the constraints imposed by the absence of both a capture web (spun by most other social spiders) and a silken nest (spun by all other social spiders, including *Diaea*), allowing these spiders to derive benefits of group living similar to other social spiders? (2) If not, what other benefits might have selected for group living in this species? We specifically examine cooperative defense and cooperative foraging, two benefits of group living that are important to a wide variety of social animals (e.g. Buskirk 1981; Macedonia & Evans 1993; Baird & Dill 1996; Breed et al. 2004; Yorzinski & Vehrencamp 2009). To accomplish this, we performed two sets of introduction experiments: (1) We introduced potential predators into field and laboratory retreats and recorded which spiders responded aggressively. (2) We introduced potential prey items into field retreats and recorded which spiders captured the prey and whether the prey was subsequently shared. In addition, we examined naturally occurring prey capture both inside and outside field retreats, recording the amount of prey captured in the presence of other spiders and whether spiders gained prey cooperatively. We employed a novel method for observing field colonies inside the retreat, allowing for observations that were both as unobtrusive and in as natural a setting as possible.

Because *D. cancerides* lacks a capture web to facilitate recruitment to predators or prey, we predicted active cooperation to be rare and for spiders to capture prey individually. However, based on laboratory observations, we expected prey sharing to provide an important component to the juvenile diet. As *D. cancerides* colonies typically contain multiple cohorts of different aged spiders

(Rayor et al. in prep.), we predicted the older siblings to maximize their inclusive fitness by sharing their prey and protecting the younger brood.

Methods

Study organism and study sites

Delena cancerides is endemic to Australia (Main 1962). Field observations were conducted at Mt. Ainslie, Canberra, Australia from 8 Oct. 2006 through 1 May 2007 and from 2 Feb. through 19 April 2008. Laboratory observations were conducted at Cornell University, Ithaca, NY, USA from 24 June until 11 July 2008. Colonies can consist of up to 300 individuals (Rowell & Avilés 1995), but the average colony size in this study is 22.6 individuals for field colonies and 27.0 for laboratory colonies. Most colonies have only one resident adult female, but 2-3 adult females are occasionally collected from the same retreat. Based on the condition of the cuticle (cuticle color and wear of cuticle hairs give an indication of spider age), these females are probably one older adult female that is the mother of one or two recently matured daughters. All but one field colony observed in this study had only a single adult female, presumed to be the mother of all the offspring. One colony was an orphaned colony, containing subadults and younger spiders, but no adult female. Female spiders have 10-11 instars, though males may have fewer. Because body size strongly correlates with prey size in spiders (Buskirk 1981), we divided immature spiders into two size categories: 'juveniles' refers to spiders sixth instar and younger, while the readily sexed seventh to ninth instars are termed 'subadults.' For analyses, adult males were grouped with subadults because both categories of spiders were similarly sized. The number of males was too few to compare analytically to subadults, but in the few trials with adult males, they behaved similarly

to subadults (see results and Figs. 2-5). Colony demographics change not only over long periods of time but also from night to night, depending on the number of spiders that might be out foraging. Since not all tests were conducted simultaneously, colony demographics differ from test to test and are reported separately.

Retreat manipulation

To observe the defensive and foraging behaviors of spiders in the field, it was necessary to modify their retreats in such a way that allowed the retreat to be opened to observation with as little disturbance to the spiders as possible while maintaining the protective integrity of the bark. To this end, we constructed 'retreat windows' in natural bark retreats. Two forms of retreat windows were used to view inside established colonies. Both forms of retreat windows involved cutting viewing holes in the external bark. To create retreat windows in occupied retreats in 2006/7, holes were cut in the bark of 21 colony retreats using a battery-powered rotary saw, and a thin (< 0.5 mm) sheet of clear plastic was glued over the hole using polyepoxide. The piece of bark removed from the retreat was then reattached to the retreat with string so that it covered the window and could be easily removed at night for viewing nocturnal activity within the colony (Fig. 1a). A thick fabric sheet between the cover and the window helped seal cracks from light and maintain a tight fit between window and cover. All retreats were given at least two windows, installed over at least 2 days, so that spiders could move to another portion of the retreat while each window was made. Window size varied and was dictated by the size of the bark that sheltered colonies (Fig. 1). In 2008, we collected 14 entire spider colonies along with their bark and moved them to the laboratory. A single, large window was cut into each piece of bark (Fig. 1 b, c, d). An acrylic sheet (0.5 mm thick) was bolted to the bark, and the edges sealed with silicone sealant. Retreats

were reattached to trees with hook and loop fasteners (Velcro), and the cover was attached with Velcro with a sheet of black fabric between the cover and window. Spiders from each colony were given colony-specific marks with Testors enamel paint applied to the carapace and sternum, fed, and returned to the field within 48 h of collection. The bark with the retreat window was reattached to the tree, and spiders were gently coaxed back into the retreat. To enhance retention of the spiders while they readjusted to the modified retreat, the entire retreat was enveloped in 2-3 layers of nylon tulle for at least 3 days. Both processes were clearly disruptive to spiders. Of 21 retreats given windows in 2006/2007, 10 were abandoned within 2 weeks. Of 14 retreats in 2008, 6 were abandoned within 3 days. However, colonies in which individuals remained together under the modified bark remained viable for months (some for over a year). We observed a total of 19 colonies that successfully remained under retreat windows.

While disruptive to the spiders, we believe the retreat windows present an accurate representation of field behavior for two reasons. (1) We have also observed behavior on un-manipulated field retreats. In both manipulated and un-manipulated retreats, some portion of colony leaves the retreat to forage at dusk and returns at dawn. While the precise percentage of the colony foraging is only known in manipulated retreats, the numbers of spiders seen leaving manipulated retreats are consistent with the numbers leaving un-manipulated retreats (average number of spiders leaving un-manipulated retreats: 3.33 ± 0.96 S.E.; average number of spiders leaving manipulated retreats: 3.98 ± 0.81 S.E; mean % of the colony leaving = 15% ± 14 S.D.). All ages over second instar were seen leaving both types of retreats, though in both cases, most spiders were fourth to sixth instar. (2) Observations on the 19 manipulated colonies were taken 1-136 days after the retreat

had been altered. There was no relationship between time post-disruption and the percentage of the colony leaving the retreat to forage (GLM with colony as a random effect, t = 0.31, p = 0.76, n = 31), whether each age class of spider attacked the predator (logistic regression adult females χ^2=0.01, p = 0.91, n=34; subadults χ^2=1.54, p = 0.22, n=19; juveniles χ^2=0.58, p = 0.45, n=37), or which age class of spider captured the introduced cricket (logistic regression, χ^2=1.04, df = 2, p = 0.59, n=24). Given that manipulated colonies (1) showed minimal differences from non-manipulated colonies and (2) were consistent over time, there is no evidence to suggest that these spiders behaved differently than those in un-manipulated colonies.

Predator introductions and defense observations

Predation on *D. cancerides* spiders is not easily observed. However, spider numbers in colonies gradually decline over time, and solitary individuals younger than the penultimate instar are rarely collected in the field (Rayor et al. in prep.), suggesting that mortality and predation may be common. Only three predation events have been directly observed: two instances of cannibalism (one inside and one outside the retreat) and one instance of an adult solitary huntsman spider (*Pediana regina*) capturing a fifth instar *D. cancerides* spider foraging outside the retreat. However, indirect evidence indicates that other species of solitary huntsman spiders and ants are likely predators. The remains of dead *D. cancerides* spiders have been found in neighboring solitary huntsman retreats (L. S. Rayor pers. obs.). Occasionally, when spiders escaped to the ground while being collected they were attacked by large numbers of ants (unidentified species). Brown bulldog ants (*Myrmecia pyriformis*) were twice observed invading *D. cancerides* colonies. In one instance, the resident adult female survived with her offspring. In another instance,

the retreat was found abandoned and filled with debris by the following observation, and *M. pyriformis* ants were seen on or in the retreat for the following week. In another instance, a recently abandoned retreat was found with 6 dead *M. pyriformis* ants at the bottom, and *M. pyriformis* ant heads have been found at the bottom of other *D. cancerides* retreats.

Because of these observations, we introduced *M. pyriformis* ants and three species of sympatric solitary huntsman as potential predators into retreats in the wild and in the laboratory, and detailed the resulting behavior of the spiders. Nineteen *M. pyriformis* ants, 12 *P. regina* (Sparassidae) adult females, and 6 *Isopedella pessleri* (Sparassidae) males and females were collected on Mt. Ainslie and introduced into *D. cancerides* field colonies. Each colony was tested with one ant and one solitary huntsman, in a random order, and each trial was separated by at least 24 h. *Pediana regina* and *I. pessleri* adults are considerably smaller than an adult *D. cancerides* (mean carapace length for *P. regina* = 6.7 mm, Hirst 1989; *I. pessleri* = 8.6 mm, Hirst 1993; *D. cancerides* = 10.6 mm, E. C. Yip unpubl. data). To test how spiders might respond to a larger solitary huntsman, 14 large *Holconia flindersi* penultimate and adult spiders (mean carapace length of these laboratory animals = 10.72 mm; unpubl. data) from a laboratory population were introduced into laboratory colonies of *D. cancerides*. Three or more species of *Holconia* are found in much of *D. cancerides*' range in southeastern Australia, but not at our specific study sites in Canberra. Laboratory colonies were housed in glass terraria with clear acrylic sheets serving as retreats using the methods described in Yip et al. (2009). The *H. flindersi* spiders were offspring of animals collected in South Australia in 2006 and raised in the laboratory. Laboratory colonies of *D. cancerides* were collected from 4

sites across southern Australia: two in the Australian Capital Territory, one in New South Wales, and one in Victoria.

Predator observations followed the following protocol: Predators were transported from the field or laboratory in plastic vials and then gently coaxed into the retreat entrances, which are usually restricted to one or two small openings by silk. While this does not present all spiders with an equal opportunity to encounter the predator, it presents a realistic scenario, as invertebrate predators, like the ones used in this study, almost certainly enter the retreat through these entrances. Predators and spiders were observed for 1 h or until the predator was killed. We recorded our observations in a hand-held tape recorder. To ensure that predators encountered as many spiders as possible, predators were not allowed to leave the retreat. Spiders were considered to have 'contacted' a predator when they physically touched. Following contact, responses to the predator were classified as 'ignore,' defined as no action or slow movement away from the predator; 'investigate,' defined as tapping or following the predator without attacking the predator; 'attack,' defined as lunging, biting, or attempting to bite the predator; 'retreat,' defined as rapid movement away from the predator; and 'kill.' Attacks did not always result in mortality, but all spiders that 'killed' were also considered to have 'attacked.'

Responses among age groups were compared using Kruskal-Wallis Rank Sum Tests followed by Tukey-Kramer comparisons. For each trial, we scored whether individuals engaged in the behaviors defined above as yes/no. We calculated the percentage of individuals of a given age group engaging in a behavior and use these percentages as the unit of replication. The number of individuals in a given age group varied from trial to trial. Because percentages generated from trials

with many individuals are a more reliable representation of spider behavior than percentages generated from only one or two individuals, data were weighted by the number of individuals in each age group able to participate in a given behavior. For example, data comparing rates of contact were weighted by the total number of individuals in each age group in the colony, while data comparing rates of attacking were weighted by the number of individuals in each age group that contacted the predator.

Foraging observations

We examined possible benefits of group foraging in two ways in the field: observing natural prey capture and spiders' reactions to house crickets (*Acheta domesticus*) that were provided. Natural prey capture was observed both inside and outside the retreat. For prey capture inside the retreat, the 19 colonies with retreat windows were observed repeatedly over 68 nights for a total of 313 h. For prey capture outside the retreat, spiders seen leaving the 19 colonies with windows, plus an additional 2 colonies without windows, were tracked on foot over the same 68 nights for a total 134 h. We recorded all instances of spiders attacking or feeding on prey, including data on the approximate instar of the feeding spider, the approximate prey length, and the taxonomic order of the prey. We used the average weights of instars collected from the field (E. C. Yip unpubl. data) to estimate the weights of feeding spiders. Prey length and order were used to approximate prey mass using the methods of Sage (1982). We calculated the rates of prey capture inside and outside the retreat by dividing the total weight of prey captured by the number of spiders observed and by the hours of observation for each spider ('spider-hours'). All spiders within a given retreat were observed simultaneously. The number of spiders in the retreats varied from colony to colony and from one observation period

to another. To calculate the total number of spider-hours inside the retreat, we multiplied the number of spiders in the retreat by the duration of the observation period. These were then summed over all observation periods for a total of 6,474 spider-hours inside the retreat. Most observations outside the retreat were on a single spider, but rarely two or three spiders were close enough to be observed simultaneously. The focus required to track a single individual made recording exact time intervals on secondary spiders impractical. Instead, the total mass of prey captured outside the retreat is divided by two spiders for a total of 268 spider-hours, creating a conservative estimate of prey capture outside the retreat.

Generally, we had only one observer in the field at a time, so only one colony or spider out foraging could be observed at a time. Observation time was divided between inside and outside the retreats using the following protocol: Observations began at one retreat 15 min prior to sunset each evening. The first spider leaving the retreat to forage was then tracked on foot until it could no longer be sighted. The duration of tracking on an individual spider varied considerably, from 15 min to over 10 h. Subsequent spiders seen foraging outside were also tracked for prey capture until lost. When not tracking spiders outside the retreat, we opened retreat windows and observed spiders inside for any prey captured within the retreat.

To further examine the possibility of cooperative foraging, we introduced house crickets into colonies. Prey could be captured at the retreat in two ways. Prey might wander into the retreat, or prey might alert spiders from outside the retreat entrance. To mimic these two situations, 18 crickets were placed inside the retreat. An additional 10 crickets were held (either manually or attached by sticky gum) at an entrance to the retreat of 10 colonies. The cricket's legs were allowed to scrape against the bark to cause vibrations, to which spiders might respond. We recorded

the approximate age and sex of spiders that contacted, ignored, investigated, attacked, and killed the cricket (as defined in our predator observations) and whether the cricket was shared, and with which spiders, within 1 h of capture. As with the predator trials, all observations on prey capture were recorded with a tape recorder. We use the same analyses described under predator observations to compare the behaviors of different age groups.

While house crickets are not part of *D. cancerides*' natural diet, their commercial availability allowed for easy replication of introductions, and spiders in the laboratory readily prey on them (L. S. Rayor unpubl. data). Crickets were adult and subadults (~2-2.5 cm). All colonies contained at least one spider large enough to capture the cricket on its own based on laboratory observations (either adult or subadult spiders).

Results

Predator introductions and defense observations

Delena cancerides age groups varied in their responses toward predators (Figs. 2-4). Adult females killed 23 (55%) of the 42 predators introduced into a colony with an adult female present. Thirty-two (63%) of 51 predator introductions were in colonies with subadults and/or adult males, but only once did a subadult successfully kill a predator. No juvenile killed a predator. These differences among age groups in killing predators were the result of differences in their probability of contacting, their propensity to attack, and their capacity to kill predators.

Adult females were more likely to contact *M. pyriformis* ants than subadults/males or juveniles (Kruskal-Wallis Rank Sum Test followed by Tukey-

Kramer Comparison: χ^2=26.74, df=2, p<0.0001, n=47). There were no other significant differences in the rate of contact among age groups for other predators.

After initial contact, adult females were the most aggressive age group and attacked predators in all but one case. Subadults and adult males attacked *M. pyriformis* ants if directly threatened (n=12 instances over 4 trials), but they uniformly ignored the small *P. regina* and *I. pessleri* huntsman. They occasionally attacked the larger *H. flindersi* huntsman but most often ignored them. A small number of juveniles (third-sixth instar) attacked all predator types (n = 21 instances over 7 trials), but were more likely to investigate, ignore, or retreat from predators (Figs. 2-4). Adult females were more likely than subadults/males and juveniles to follow contact with an attack against both the small solitary huntsman (Kruskal-Wallis Rank Sum Test followed by Tukey-Kramer Comparison: χ^2=15.39, df=2, p=0.0005, n=25) and the larger *H. flindersi* (Kruskal-Wallis Rank Sum Test followed by Tukey-Kramer Comparison: χ^2=9.69, df=2, p=0.0079, n=21). Both adult females and subadults/males were more likely than juveniles to attack *M. pyriformis* ants following contact (Kruskal-Wallis Rank Sum Test followed by Tukey-Kramer Comparison: χ^2=23.68, df=2, p<0.0001, n=38).

Once they attacked potential predators, adult females were the most effective at killing them. They not only overpowered the predators more easily, but were also more tenacious in their attacks. When encountering the formidable *M. pyriformis* ants, adult females sometimes retreated, but reengaged the ant until they killed it (Fig. 2a). Only one adult female, after engaging the ant and retreating twice, failed to kill the ant during the observation period. By contrast, after the initial attack subadults (and the single adult male that contacted the ant) usually ran and avoided future contact with the ant (Fig. 2b). This resulted in attacks by adult females killing

more ants than attacks by subadults/males (Kruskal-Wallis Rank Sum Test: χ^2=7.26, df=1, p=0.007, n=22). Attacks by juveniles were ineffective at killing predators. Their lighter bites appeared to not pierce the cuticle, as no hemolymph was ever seen to bead from a wound caused by a juvenile. Instead, bites sometimes caused the predators to flinch or startled them into running. Unlike field trials, no spider successfully killed an *H. flindersi* spider due to the latter's size and speed (Fig. 4).

Multiple spiders cooperating in the defense against predators was very rare. In all trials, spiders running away from the predator precipitated other spiders to run or adjust their position. However, there was no obvious evidence that spiders recruited nestmates to attack the predator, nor was there indication that spiders running in response to sibling contact moved to a particular safe location away from the predator, near the mother, or in tighter areas under the bark. Of all predator introductions, only one predator (an ant) was attacked simultaneously by multiple individuals for more than a few seconds. It was attacked by all spiders it contacted, (12 fourth-fifth, 1 sixth, and 3 seventh instar spiders, with as many as 5 juveniles all attacking at once). The ant was eventually killed by the adult female.

Foraging observations

Delena cancerides spiders are nocturnally active, and spiders depart from their retreats at dusk to forage. They would occasionally return to the retreat in the middle of the night, but the majority only returned at dawn the next day. Second instars (the first instar out of the egg sac which does not feed) were never seen leaving the colony. Third and fourth instars left the retreat but tended to remain on the natal tree. Older instars usually headed directly to the ground upon leaving the retreat. They wandered erratically 3-10 m net distance from the retreat before climbing a tree. Short trees and shrubs (2-3 m in height) were explored but usually abandoned.

When spiders climbed tall trees, they were visually lost after reaching ~4 m above the ground. We successfully followed only two spiders for the entire night. Only a small number of the spiders in each colony left the retreat each night (mean = 15% ± 2% S.E., range = 0%-43%). When not foraging, spiders remained in the retreat, with the exception of short periods to defecate, to molt, or to dispose of old molts.

Spiders captured a total of 64 prey items in the field, ranging from 1-11 mm in length. Two of these were instances of cannibalism (by an adult female eating a subadult female inside the retreat, and by a seventh instar eating a fourth instar outside the retreat) and are not included in the total prey mass captured. Spiders fed on ants (n = 16), flies (n = 7), homopterans (n = 7), beetles (n = 5), roaches (n = 3), moths (n = 3), lepidopteran larvae (n = 3), a non-formicid hymenopteran (n = 1), and an oxyopid spider (n = 1). Sixteen prey items were too small and/or too masticated to be identified. The estimated average weight of prey was 6.7 mg, median 1.2 mg, with the largest prey item being an 11 mm fly that weighed an estimated 137 mg based on Sage's (1982) biomass equations. Prey items averaged 6% (± 3% S.E.) of the estimated weight of the capturing spider. Only 5 of 62 prey items (cannibalism excluded) were captured inside the retreat, totaling an estimated 22 mg. The estimated consumption rate inside the retreat is 0.0034 mg/spider/hr. Of these 5 prey items, only 1 was shared (by six fifth instar juveniles). The remaining 57 prey items were all captured outside the retreat, totaling an estimated 393.4 mg. The estimated rate of consumption outside the retreat is 1.47 mg/spider/hr. Spiders consumed the majority of prey captured outside the retreat at or near the site of capture. However, spiders feeding at dawn did return to the retreat with prey. Of the 57 items captured outside, 9 were brought into the retreat at dawn. Whether these prey items were subsequently shared is unknown. By the time the spiders returned

at dawn it was too bright to keep the retreat windows open, and if they were left open, spiders hid along the edge of the windows out of view.

The placement of the cricket either inside the retreat or at the retreat entrance had no effect on the probability of spiders contacting the cricket (GLM with spider age group as a co-variable: F ratio=0.79, p=0.38, n=63), the probability of attacking the cricket once contacted (GLM with spider age group as a co-variable: F ratio=0.13, p=0.72, n=36), or the probability of killing the cricket once attacked (GLM with spider age group as a co-variable: F ratio=0.36, p=0.55, n=32). Therefore data from the two types of cricket placements are pooled for further analyses. Of 28 crickets, 3 escaped after 1 h of observation. Of the remaining 25 crickets, most (21) were captured by adult females (Fig. 5). One was captured by an adult male, and two were captured by subadults (one male and one female) in the 12 trials in which the cricket was captured and colonies contained subadults and adult males (Fig. 5). One was captured by a group of third instar spiders; however, this particular cricket was affixed at the entrance to the retreat by gum. While this shows that spiders as young as third instars attack prey wandering near the entrance of the retreat, it seems unlikely that the third instar spiderlings could have captured a cricket of this size had it been able to escape. For the purposes of analyses, these spiders are considered to have attacked but not killed the cricket. Adult females were more likely than subadults/males and juveniles to make contact with the cricket (Kruskal-Wallis Rank Sum Test followed by Tukey-Kramer Comparison: χ^2=26.16, df=2, p<0.0001, n=66). Both subadults and juveniles were less aggressive toward crickets than adult females, in that they occasionally ignored or investigated crickets without attacking while all adult females attacked the cricket if they came into contact with it (Kruskal-Wallis Rank Sum Test followed by Tukey-Kramer Comparison: χ^2=11.84,

df=2, p=0.0027, n=36). Even when they did attack, single juveniles were unable to capture prey as large as the crickets. Subadults and adult males captured the crickets nearly as often as they attacked them (Fig. 5b).

Eleven of 21 crickets (52%) captured by adult females were shared with juveniles (third-fifth instar) at some point during the first hour after capture (Fig. 5). The adult female initially appeared reluctant to share prey, often batting juveniles away with her legs and securing prey for herself if she could. Adult females and the 3 subadults/males that captured crickets were forced to share more often in trials with more juveniles present (logistic regression: $\chi 2 = 4.28$, df = 1, p = 0.039, n= 24), as the number of actively soliciting juveniles overwhelmed their defenses. Young *D. cancerides* juveniles have a distinctive solicitation behavior and will often attempt to share prey held by other individuals (L. S. Rayor unpubl. data). We never observed subadults sharing or attempting to share with adult females. There was a single instance when subadults shared with another subadult and one juvenile (Fig. 5), but no other subadults were ever seen sharing prey.

Discussion

Our study examined two potential benefits of group living, cooperative defense and cooperative foraging, to determine whether these are major payoffs supporting sociality in *D. cancerides*, given the constraint that they lack a web. We had predicted that, even without a capture web, older siblings would help defend the colony and that spiders would capture prey individually but share with nestmates. Instead, our data show that, other than the adult female, spiders generally acted individually when defending themselves from predators or obtaining food. Maternal defense and prey sharing provided some benefits from remaining in the natal retreat.

Overall, *D. cancerides* spiders do not derive the same defense and foraging benefits as most of the web-based social species, yet they have evolved to live in groups despite lacking a parallel mechanism to mediate cooperative prey capture or defense.

One clear benefit of staying in the natal retreat demonstrated by our data is maternal defense. The adult female was far more aggressive and effective in eliminating potential predators than any other spider in the colony. While all offspring benefited from maternal defense, the relative benefits were almost certainly greatest to smaller spiders that are less able to defend themselves. Contrary to our prediction, spiders derived no similar benefit from older siblings. The subadults were ineffective in eliminating predators, even though subadults (seventh through ninth instar) are in the same size range as the smaller species of solitary huntsman in the area (*P. regina* and *I. pessleri*) and larger than other potential predators such as *M. pyriformis* ants.

We observed one remarkable instance in which multiple spiders mobbed a single predator (*M. pyriformis* ant), which suggests the possibility that spiders may together drive away predators too large for a single spider; however, such mobbing behavior appears to be very rare. In other organisms, such mobbing behavior is sometimes accomplished through the active recruitment of other group members to the threat (Macedonia & Evans 1993; Breed et al. 2004; Yorzinski &l Vehrencamp 2009). In this case, however, spiders persistently (though ineffectively) attacked the ant only when it contacted each particular spider, so that the ant accumulated attackers as it moved through the retreat. Thus, this one instance of mobbing was not an example of active recruitment, but rather the result of spiders displaying persistent aggression not seen in other predator trials.

In web-building social spiders, vibrations sent through the web can act to recruit spiders to defend against a large predator (Vollrath & Windsor 1983) or as an advanced warning system (Hodge & Uetz 1992). Even without a web, spiders are known to communicate both chemically (Gaskett 2007) and acoustically (Hebets & Uetz 1999; Elias et al. 2005). However, despite the ability to communicate, we found no obvious evidence that *D. cancerides* spiders recruited other individuals to aid in an attack on a predator or to emit signals with information about the nature or direction of the threat. Our study did not explicitly examine passive defense benefits, such as the selfish herd (Hamilton 1971), nor was our study designed to detect information spiders might convey that results in very subtle changes in spiders' behavior. Thus, while our data show active cooperation in predator defense is very rare, we cannot rule out other defensive benefits they might derive from living in groups.

In other social spider species, silk acts as a barrier to predation, and this barrier improves as colony size increases (Rayor & Uetz 1990; Uetz & Hieber 1997; Evans 1998). *Delena cancerides* spiders, however, probably do not derive a similar benefit of group living. The bark retreat of a *D. cancerides* colony is sealed around the edges with silk, with only one or two entrances that are usually just large enough to accommodate the adult female spider that frequently stands at the entrance (pers. obs.). This severely restricts access to the retreat by predators. We witnessed no natural predation within the retreat besides one instance of cannibalism, suggesting that the retreat acts as an effective barrier to most predators. Most predation probably occurs outside the retreat while spiders forage individually and is therefore unassociated with either group size or retreat size. Unlike a web, which increases proportionally as colony size increases in other social spiders, the bark does not

increase in size or improve as a barrier to predation as the number of spiders in the colony increases. Indeed, the opposite may be true, in that the area under a given piece of bark may fail to accommodate all spiders, especially as the young mature and increase in size.

The importance of prey, as a resource both gained cooperatively and contested competitively, has garnered considerable attention in the social spider literature. Several studies have suggested that competition for prey intensifies as colonies grow larger, and prey intake fails to keep pace (Ward 1986; Seibt & Wickler 1988; Rypstra 1993), while other studies show group living increases individual prey capture success (Uetz 1988; Uetz 1989) or the size of the insects captured (Ward 1986; Jones & Parker 2002; Yip et al. 2008), providing a net benefit for spiders, within a certain range of colony sizes (Yip et al. 2008). Yip et al. (2008) further suggest that the cooperative capture of large prey and the presence of large prey in the environment are key to the distribution of sociality in the genus *Anelosimus*. Whether social foraging provides a net benefit or cost and what role social foraging plays in the evolution of group formation and size have generated debate in the social vertebrates as well (e.g. Packer et al. 1990; Creel & Creel 1995; Creel 1997; Packer & Caro 1997). The balance between cooperation and competition in securing prey appears to be of far less importance in *D. cancerides*, as spiders gain the vast majority of their food resources away from the retreat, where spiders have no opportunity to interact with any frequency.

Contrary to our predictions, prey sharing appears to be relatively rare. Only juveniles regularly shared the prey that was captured inside the retreat, only about half of prey captured inside the retreat was shared, and spiders captured over 431 times as much prey mass outside as inside the retreat. Using these data, only an

estimated 0.1% of prey mass is shared with other spiders. Furthermore, the spiders exhibited behaviors that limited prey sharing. Adult females usually attempted to brush juveniles away from the prey item. After capturing crickets within the retreat, two spiders left the safety of the retreat to feed outside alone. Whether prey brought back to the retreat at dawn is subsequently shared is unknown, but spiders returning with prey appeared reluctant to enter the retreat, instead preferring to continue to feed near the retreat entrance or only half inside, with the prey item outside and shielded from other spiders by the body of the feeding spider. However, we cannot rule out the possibility that sharing even small amounts of prey may be an important benefit to younger spiders that have a more limited capacity to capture prey on their own, particularly larger prey items. Subadults appear to gain virtually no benefits from group foraging.

Compared to the more advanced web-building social spiders (see reviews by Avilés 1997; Lubin & Bilde 2007), active cooperation in *D. cancerides* is limited in terms of foraging and defense, and spiderlings benefited most through the presence of the mother rather than from siblings. This supports the hypothesis that the absence of the web acts as a constraint, not necessarily for group living, but certainly for certain cooperative behaviors in the spiders. However, group living in *D. cancerides* cannot be attributed to maternal care alone, as orphaned colonies (lacking an adult female) are known to persist for months. We argue two reasons for the persistence of these groups. (1) Spiders delay dispersal because the relative costs of group living are low. Although older spiders may not benefit from cooperative prey capture or share to any great extent in the field, neither do they suffer from intense food competition within the colony. Thus, the absence of a capture web in *D. cancerides* may act as a double edged sword in social evolution:

while it limits the extent of cooperative behaviors that in turn mitigate the costs of group living, it also frees spiders to forage outside the limits of a web and away from close relatives. (2) Under the ecological constraints hypothesis (Emlen 1982), habitat saturation is known to promote group living in a variety of species, including birds (Komdeur 1992; Kappes 2008), fish (Wong 2009), mammals (Blumstein & Armitage 1999; Schradin et al. 2010), and ladybeetles (Honěk et al. 2007), but has never been documented for a social spider. The bark retreats these spiders require to successfully breed appear to be quite rare, with colonies occupying near 100% of suitable retreats at many collection sites (Rayor et al. in prep.). Further, laboratory data show that larger *D. cancerides* adult females almost always push smaller adult females out of artificial retreats (Yip and Rayor see Chapter 5). Dependence on a rare retreat may then have allowed evolution to circumvent the web in selecting for group living, as spiders remain in their natal retreat until adulthood because dispersing at a smaller size would put them at a competitive disadvantage for securing an unoccupied retreat. We are currently conducting a field experiment examining the relationship between retreat abundance and occupancy of artificial retreats to test this hypothesis.

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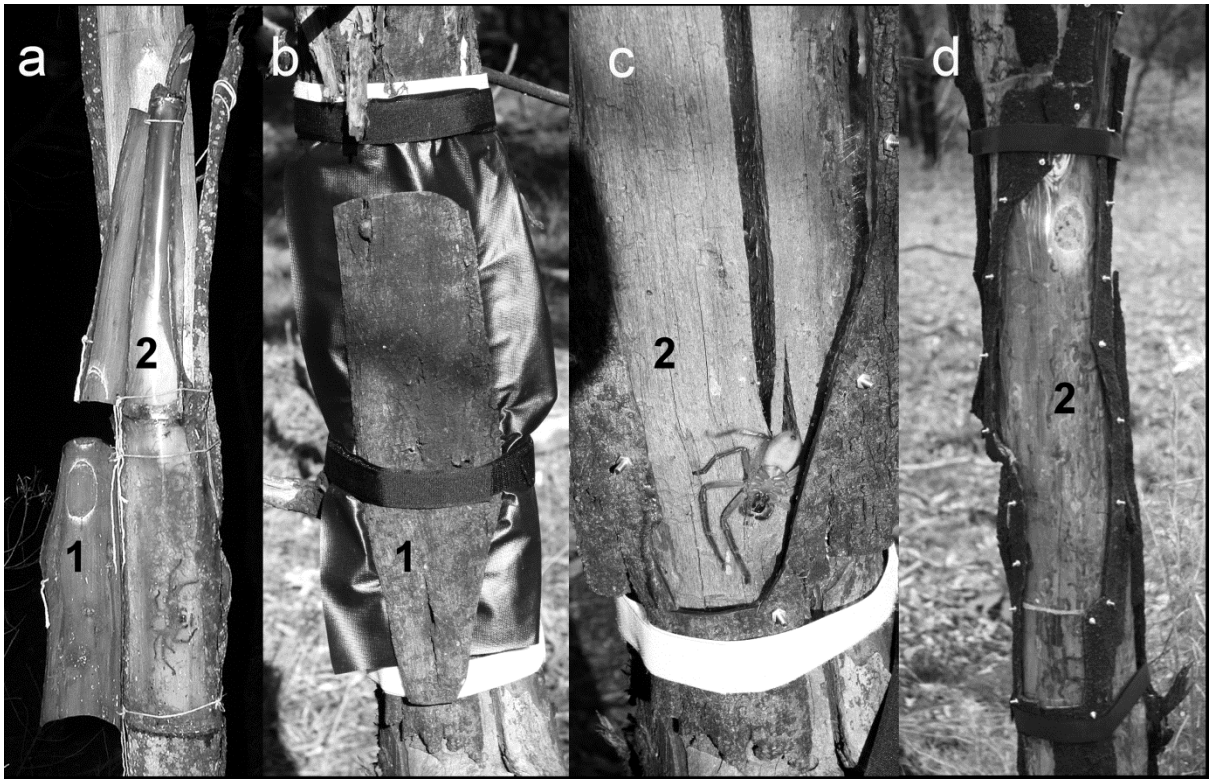


Figure 1. Photographs of retreat windows in 2006/7 (a) and in 2008 (b, c, d). The number 1 designates the bark cover, and the number 2 designates the clear plastic window for both types of retreat windows. Bands of Velcro help hold the retreat window tightly onto the tree (b,c,d). Note the adult female and offspring in (a) and adult female in (c).

Figure 2

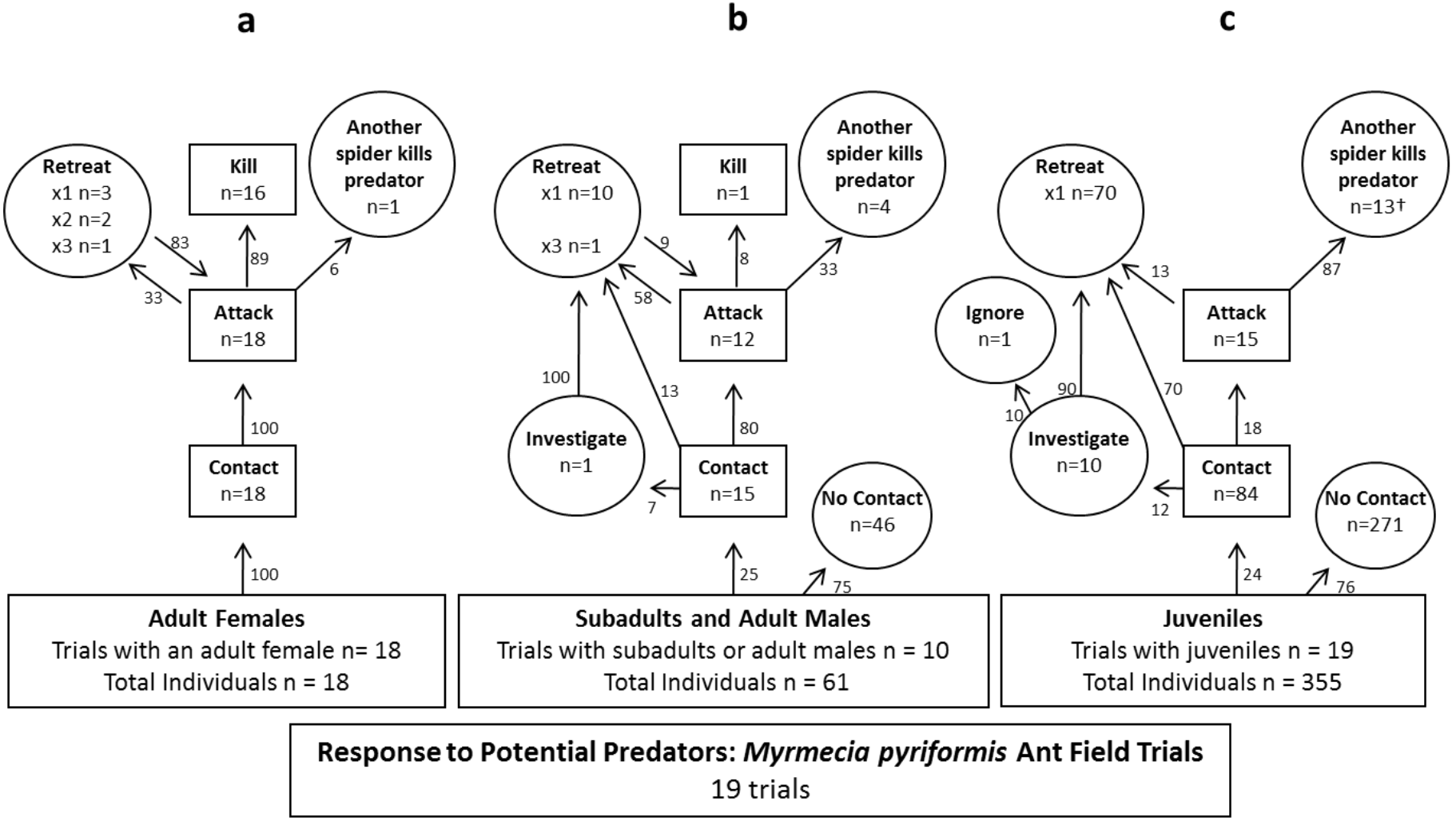
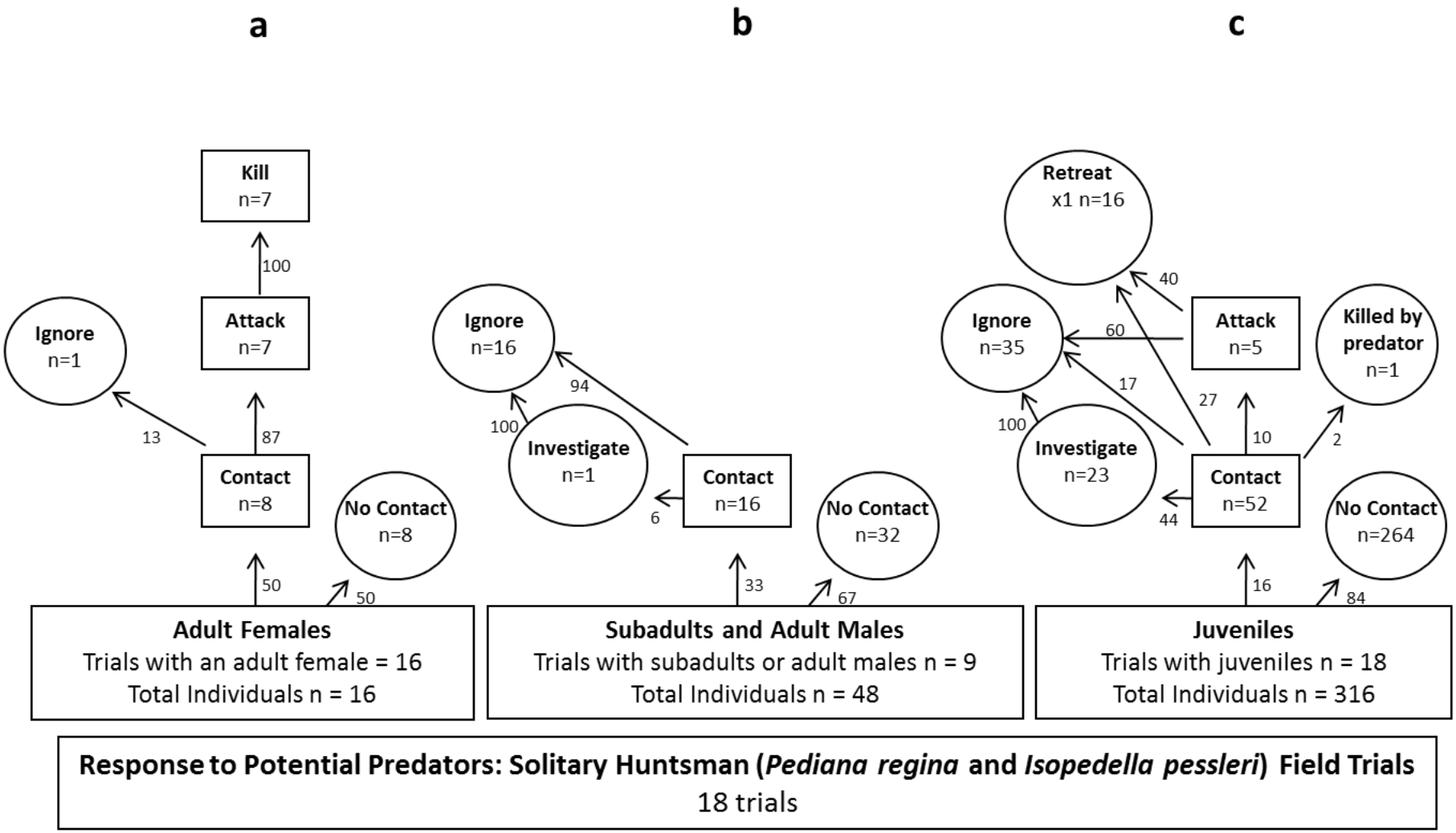

a
b
c
Retreat
x1 n=3
x2 n=2
x3 n=1
Kill
n=16
Another spider kills predator
n=1
83
89
6
33
Attack
n=18
100
Contact
n=18
100
Adult Females
Trials with an adult female n= 18
Total Individuals n = 18
Retreat
x1 n=10
x3 n=1
Kill
n=1
Another spider kills predator
n=4
9
8
33
58
Attack
n=12
100
13
80
Investigate
n=1
Contact
n=15
7
No Contact
n=46
25
75
Subadults and Adult Males
Trials with subadults or adult males n = 10
Total Individuals n = 61
Retreat
x1 n=70
Another spider kills predator
n=13†
13
87
Ignore
n=1
Attack
n=15
90
70
10
Investigate
n=10
18
Contact
n=84
12
No Contact
n=271
24
76
Juveniles
Trials with juveniles n = 19
Total Individuals n = 355
Response to Potential Predators: *Myrmecia pyriformis* Ant Field Trials
19 trials

Figure 2. A flowchart of (a) adult female, (b) subadult and adult male, and (c) juvenile behavior in response to the introduction of *M. pyriformis* ants into field colonies. n indicates the total number of spiders of that age group engaging in the behavior summed over all trials. Numbers adjacent to arrows indicate the percentage of spiders in the previous box moving down that behavioral path. The multiplier under 'Retreat' indicates the number of times a particular individual retreated from a single predator. Of the 61 subadult and adult male spiders, 5 were adult males. One adult male contacted the ant, attacked, then retreated. The † indicates that 13 juveniles were from a single exceptional trial (A86) in which multiple juveniles attacked an ant simultaneously (see Results).

Figure 3



Response to Potential Predators: Solitary Huntsman (*Pediana regina* and *Isopedella pessleri*) Field Trials
18 trials

Figure 3. A flowchart of (a) adult female, (b) subadult and adult male, and (c) juvenile behavior in response to the introduction of solitary huntsman spiders (either *P. regina* or *I. pessleri*) into field colonies. n indicates the total number of spiders of that age group engaging in the behavior summed over all trials. Numbers adjacent to arrows indicate the percentage of spiders in the previous box moving down that behavioral path. The multiplier under 'Retreat' indicates the number of times a particular individual retreated from a single predator. Of the 48 subadult and adult male spiders, 6 were adult males. Four adult males contacted the solitary huntsman and ignored it.

Figure 4

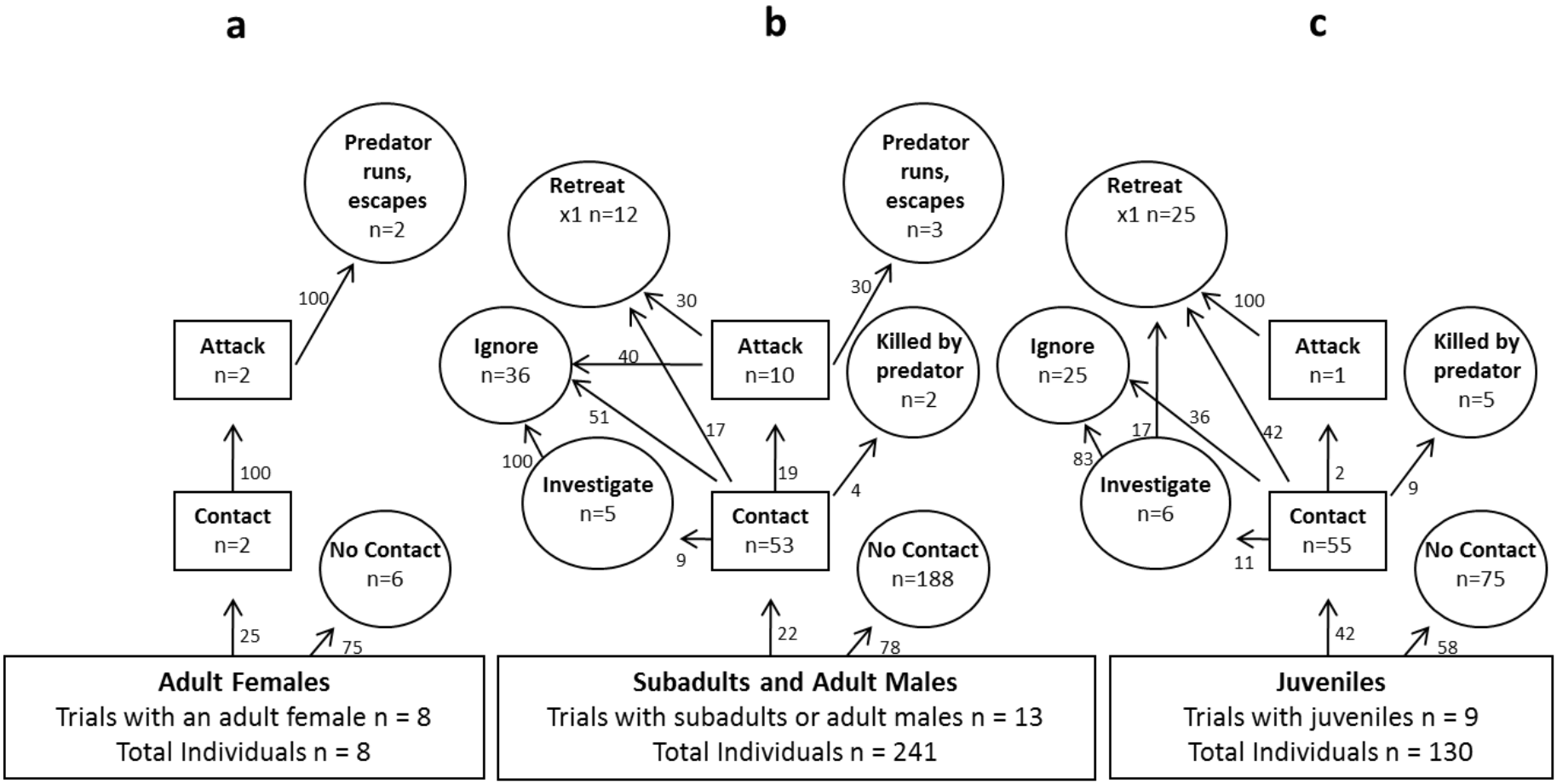

a
b
c
Predator runs, escapes n=2
Attack n=2
100
100
Contact n=2
No Contact n=6
25
75
Adult Females
Trials with an adult female n = 8
Total Individuals n = 8
Retreat x1 n=12
Predator runs, escapes n=3
30
30
Ignore n=36
40
Attack n=10
Killed by predator n=2
51
17
100
Investigate n=5
19
4
9
Contact n=53
No Contact n=188
22
78
Subadults and Adult Males
Trials with subadults or adult males n = 13
Total Individuals n = 241
Retreat x1 n=25
100
Ignore n=25
Attack n=1
Killed by predator n=5
17
36
42
83
Investigate n=6
2
9
11
Contact n=55
No Contact n=75
42
58
Juveniles
Trials with juveniles n = 9
Total Individuals n = 130
Responses to Potential Predators: *Holconia flindersi* Laboratory Trials
14 trials

Figure 4. A flowchart of (a) adult female, (b) subadult and adult male, and (c) juvenile behavior in response to the introduction of solitary huntsman spiders (*H. flindersi*) into laboratory colonies. n indicates the total number of spiders of that age group engaging in the behavior summed over all trials. Numbers adjacent to arrows indicate the percentage of spiders in the previous box moving down that behavioral path. The multiplier under 'Retreat' indicates the number of times a particular individual retreated from a single predator. Of the 241 subadult and adult male spiders, 79 were adult males. Six adult males contacted the solitary huntsman. Five ignored the predator, and one investigated it before ignoring it.

Figure 5

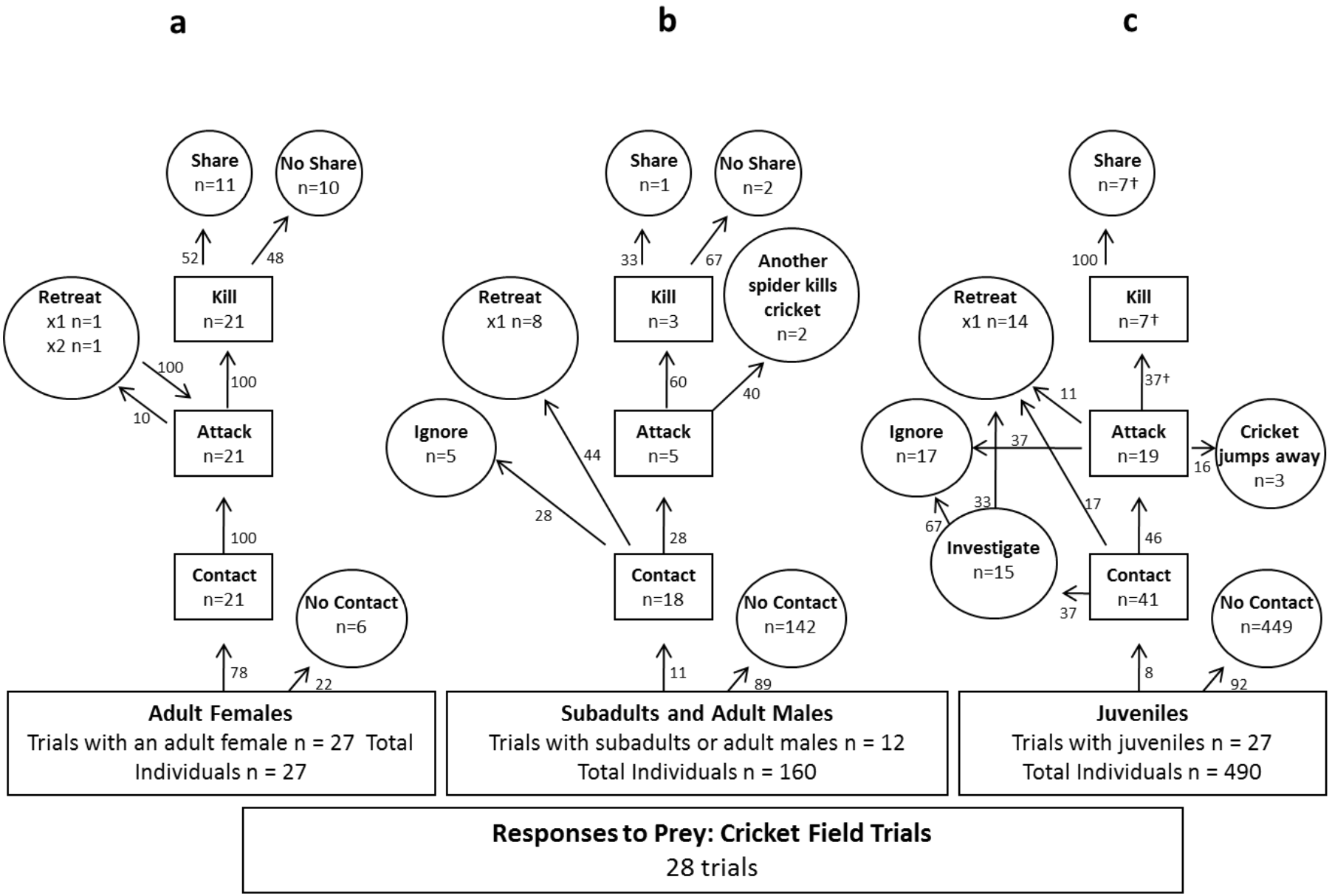

a
b
c
Share n=11
No Share n=10
52
48
Retreat x1 n=1 x2 n=1
Kill n=21
100
100
10
Attack n=21
100
Contact n=21
No Contact n=6
78
22
Adult Females
Trials with an adult female n = 27 Total Individuals n = 27
Share n=1
No Share n=2
33
67
Another spider kills cricket n=2
Retreat x1 n=8
Kill n=3
60
40
Ignore n=5
44
Attack n=5
28
28
Contact n=18
No Contact n=142
11
89
Subadults and Adult Males
Trials with subadults or adult males n = 12
Total Individuals n = 160
Share n=7†
100
Retreat x1 n=14
Kill n=7†
37†
11
Ignore n=17
37
Attack n=19
16
Cricket jumps away n=3
33
17
67
Investigate n=15
46
Contact n=41
37
No Contact n=449
8
92
Juveniles
Trials with juveniles n = 27
Total Individuals n = 490
Responses to Prey: Cricket Field Trials
28 trials

Figure 5. A flowchart of (a) adult female, (b) subadult and adult male, and (c) juvenile behavior in response to the introduction of house crickets into field colonies. n indicates the total number of spiders of that age group engaging in the behavior summed over all trials. Numbers adjacent to arrows indicate the percentage of spiders in the previous box moving down that behavioral path. The multiplier under 'Retreat' indicates the number of times a particular individual retreated from a single cricket. Of the 160 subadult and adult males, 4 were adult males. One adult male contacted the cricket, killed it, and ate it without sharing. The † indicates that all 7 of the juveniles moving down this behavioral path were from a single trial where a cricket was held at the entrance of the retreat (see Results).

CHAPTER 3

Behavioural and molecular evidence for selective immigration and group regulation in the social huntsman spider, *Delena cancerides*

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Abstract. Movement among social groups interacts with the costs and benefits of group living in complex ways. Unlike most other social spiders, the social huntsman spider, *Delena cancerides*, appears to enter foreign colonies, discriminates kin from non-kin, and has very limited dispersal options because their bark retreats are rare, making this species an interesting model organism with which to examine the role of inter-colony movement on group living. We examined movement among field colonies of *D. cancerides* in three ways: (1) by tracking the dispersal and immigration of marked spiders into foreign colonies; (2) by recording resident spiders' behaviour toward introduced immigrants; (3) by inferring intra-colony relatedness and immigration patterns through allozyme electrophoresis. Of the marked spiders, only young juveniles moved into neighbouring colonies while subadults and adults did not. Introduced juveniles were tolerated in foreign colonies while introduced adult males and subadults

were usually attacked by the resident adult female unless she had similar sized subadult/adult offspring of her own. Allozyme profiles from unmanipulated field colonies showed that 47% of sampled colonies contained at least one immigrant and that average within colony relatedness was below 0.5. These data align with previous research on the costs and benefits of group living for *D. cancerides*, suggesting that spiders actively seek and regulate group membership based on interests of both the immigrant and the colony.

Keywords: Aggression, Allozyme, Dispersal, Group Living, Immigration, Kin Recognition, Kin Selection, Relatedness, Sociality

Introduction

Movement of individuals among social groups interacts with the costs and benefits of group living in complex ways. For example, inter-group movement can change average intra-group relatedness (Gompper et al. 1997; Archie et al. 2005, Heg et al. 2011), altering the costs and benefits of social interactions via kin selection and kin competition (Hamilton 1964; West et al. 2002). Movement alters group size, which influences the degree of both cooperation and competition within the group (Chapman et al. 1995; Smith et al. 2008; Yip et al. 2008). Costs and benefits of grouping in turn feed back onto inter-group movement by selecting for the inclusion or exclusion of immigrants (Higashi & Yamamura 1993). Exclusion from groups may also make dispersal more costly in saturated habitats. For example, in some birds, older offspring delay dispersal because they are aggressively excluded from resources in occupied territories other

than their parents' (e.g. Gayou 1986; Ekman et al. 1994). Understanding whether animals can and do move among different social groups is therefore critical to understanding the costs and benefits of group living and the evolution of sociality.

Inter-group movement has been extensively described in several social vertebrates, in which groups form and disperse to suit the changing needs of individuals over time (e.g. Williams et al. 2003; Smith et al. 2008; Bercovitch & Berry 2010). Movement among colonies has also been demonstrated in social bees, in which immigration or 'drifting' may be either accidental or adaptive (Sumner et al. 2007; Beekman & Oldroyd 2008; Ulrich et al. 2009). However, such phenomena are not well documented in social spiders, which we define broadly to include any species with long-lasting associations (including species without alloparental care, such as the social crab spider *Diaea ergandros* and the colonial orb weaver *Cyrtophora citricola*). In the most highly social species that form inbred lineages, movement among colonies rarely occurs (Avilés 1997; Lubin & Bilde 2007; Agnarsson et al. 2010). Movement among groups may occur in the colonial spiders that build individual webs in dense aggregations, but little is known about their dispersal and population genetic structure (Uetz & Hieber 1997; Lubin 2010).

The social huntsman spider, *Delena cancerides* Walckenaer, is unusual among social spiders in a variety of traits which render it a useful model organism for investigating the role of inter-group movement on social evolution. First, unlike most other social spiders, genetic analyses and field observations indicate movement among *D. cancerides* colonies (Rowell & Avilés 1995; Yip & Rayor 2011). *Delena cancerides* colonies usually consist of a single adult female and multiple cohorts of young of

different ages, which have been assumed to be the adult female's offspring. However, an allozyme analysis performed on three colonies revealed that all three contained 2-4 juveniles that were not the offspring of the putative mother (Rowell & Avilés 1995). Furthermore, spiders often forage independently away from the natal retreat, with observed distances of up to 10m (Yip & Rayor 2011). As neighbouring colonies often occur within 10m or even occasionally on different sections of the same tree (Rayor et al. in prep.), spiders are likely to encounter foreign colonies and have the opportunity to enter them.

Second, *D. cancerides* faces a constraint on breeding that is exceptional among the social spiders: these non-web-building spiders only reproduce under exfoliating bark or similar narrow cavities (Rowell & Avilés 1995; Rayor et al. in prep.). Under the 'ecological constraints hypothesis' (Emlen 1982; Emlen 1995; Hatchwell & Komdeur 2000), groups form when offspring forgo or delay dispersal because the costs of solitary living are higher than those associated with staying in the natal territory. A principal component of this hypothesis is the constraint on dispersal as a result of the saturation of good breeding sites and a lack of marginal options (Brown 1974; Koenig & Pitelka 1981; Koenig et al. 1992; Hatchwell 2009). Whereas all other social spiders form colonies in webs or expandable retreats of leaves and silk (Evans 1995; Avilés 1997; Lubin & Bilde 2007), *D. cancerides* colonies are constrained by the size and availability of crevices under exfoliating bark, and retreat occupancy is over 90% in about half of all sampled populations (Rayor et al. in prep.). If spiders are aggressively excluded from neighbouring retreats, habitat saturation should constrain dispersal options and thereby increase dispersal costs.

Third, *D. cancerides* has contributed to the growing body of evidence that some social spiders can differentiate kin from non-kin (Evans 1999; Bilde & Lubin 2001; Schneider & Bilde 2008). When deprived of food, *D. cancerides* spiders preferentially cannibalized spiders from foreign colonies, indicating an ability to discriminate on the basis of relatedness or familiarity (Beavis et al. 2007). Well-fed spiders also differentiated between kin and unfamiliar (and unrelated) animals by investigating unfamiliar spiders more than nestmates (Yip et al. 2009), a common pattern among animals that recognize kin (Mateo 2004).

Fourth, spiders may regulate immigration into colonies on the basis of both relatedness and size. When aggression was observed in the laboratory, it was usually directed against larger spiders (Beavis et al. 2007; Yip et al. 2009). Data collected by Yip et al. (2009) suggested that spiders in the field may act even more aggressively than those kept under laboratory conditions. These observations indicate a capacity for spiders to control immigration into colonies.

These characteristics of *D. cancerides* suggest that spiders are capable of both seeking groups and regulating group membership. If spiders actively control immigration, we expect movement patterns to match the interests of both the immigrant and the colony into which it is accepted. In brief, previous research on the benefits of group living indicates that young spiders benefit more than older spiders by sharing prey with the mother and older siblings (Yip & Rayor, 2011; Yip & Rayor, in review, see Chapter 4). Older spiders may pose a greater threat to residents through cannibalizing smaller spiders or inheriting the retreat. Hence, we expect that young spiders will seek out groups and be accepted into them more often than larger spiders. It is currently

unknown whether immigrants are common or rare, which age of spiders immigrate, how resident spiders behave toward immigrants in the field, and whether the resulting patterns align with our understanding of the costs and benefits of group living in *D. cancerides*. To answer these questions and to deepen our understanding of the interactions between inter-colony movement and the evolution of group living, we examined inter-colony movement in *D. cancerides* in three ways: (1) by tracking the movement of marked spiders among modified field retreats, (2) recording behaviours by resident spiders toward immigrant spiders, (3) and using allozyme electrophoresis to identify migrants and estimate within colony relatedness.

Materials and Methods

Study organism and field retreat manipulation

Delena cancerides is widespread in southern Australia (Main 1962; Sharpe & Rowell 2007). Spiders live in colonies of up to 300 individuals under the exfoliating bark of primarily *Acacia* but also *Eucalyptus*, *Callitris*, and *Casuarina* trees (Rowell & Avilés 1995; Rayor et al. in prep.). Colonies usually consist of a single adult female and multiple cohorts of offspring, although occasionally two or three adult females are found in the same retreat (Rayor et al. in prep.). In this study, all 22 colonies observed in the field had a single resident adult female (colony size range: 4-40 spiders). In a separate set of 19 colonies collected for allozyme analyses, two contained multiple adult females (A5-1 and GB15). In both cases, we regarded the oldest female, based on the wear of her cuticle hairs, as the putative mother of the offspring (but see also the reported results for GB15). Offspring live together until maturity. This species appears to have

10 instars for females; perhaps fewer for males (L.S. Rayor & E.C. Yip, unpubl. data). The large, older instars (~7-9), which can be sexed, are considered 'subadults.' Younger spiders (instars 3 – 6), which cannot be sexed on the basis of external features, are referred to as 'juveniles.' These spiders emerge from the egg sac as second instars but do not feed until the third instar.

To view spiders under tree bark, we cut one or more 'windows' in the bark that forms the covering of the retreat and covered them with clear plastic (see Yip & Rayor 2011 for full details). The removed piece of bark was then secured over the plastic as a cover to keep the retreat dark except during nocturnal observations. We constructed 35 windowed colony retreats at Mt. Ainslie, Canberra, Australia, of which 19 successfully reestablished in the modified retreats and persisted for months, some for > 1 year. The remaining 16 colonies abandoned their retreats within 1 week. Eight of these 19 colonies were successfully established colonies from our marked spiders study (see below) and were used to observe introductions after the completion of the marked spiders experiment. Previous analyses indicated little difference in spider behaviour between manipulated and un-manipulated colonies (Yip & Rayor 2011).

To increase our sample size, we also successfully established three colonies in wooden nest boxes at our field site (see Supporting information, Fig. S1). These boxes were each populated with a laboratory-raised virgin female, and all offspring were produced and raised in the field. The behaviour displayed by spiders in nest boxes was consistent with spiders in modified bark retreats (see Results).

Movement of marked spiders

We collected, marked and released spiders to determine which spiders, if any, move into neighbouring colonies and to establish a minimum time that these spiders can remain in foreign colonies. Eleven colonies and three solitary adult females, totalling 432 spiders, were collected from Mt. Ainslie, Canberra, Australia from 10 February to 27 March 2008. All spiders were given colony-specific marks on both their carapace and sternum with Testors enamel paint. They were also given individual-specific marks if possible, but smaller spiders (approximately fourth instar and younger) could not be given individual-specific marks because of limited surface area. Spiders and modified retreats were returned to the field within 24 h. To minimize immediate rejection and dispersal from the modified retreats, the retreats were enveloped in two to three layers of tulle for 3-4 days while spiders adjusted to the new retreat (total time between collection and tulle removal ≤ 5 days). Colonies were collected and returned to two areas (termed 'Area1' and 'Area 2') approximately 500 m apart in similar habitats (dry sclerophyll forests, locally dominated by *Acacia* trees). To increase the chances of observing immigration into our manipulated retreats and to allow observations on more colonies in quick succession, retreats were not always returned to the tree from which they were collected. Some were moved up to 30m to areas with other *D. cancerides* colonies. Four of six colonies in Area 1 were relocated, and one of eight colonies was relocated in Area 2. No colonies shared the same tree. Colonies were not all established simultaneously: the tulle netting was removed from colonies in Area 1 on 15 Feb 2008, and in Area 2 on 16 March and 1 April 2008.

After removing the tulle and allowing the spiders free movement, these colonies with marked spiders were observed through the windows every night for 6-7 nights.

Observations began each night at sunset because spiders leave the retreat at dusk to forage and return at dawn. Whenever possible, the identity and location of spiders were recorded. We observed each window repeatedly until dawn. Although some spiders kept their marks for > 1 month after the start of observations, many of the immature spiders moulted off their identifying marks over the course of the observation period. Tracking immigration thus became more difficult to observe as time progressed and is an underestimate of the actual movement of spiders among colonies.

Immigrant introductions

To examine how colony members respond to immigrants, we introduced foreign spiders into colonies. Interactions were observed in the field through our 19 retreat windows and three nest boxes. Because neighbouring colonies are the most likely source of immigrants, introduced spiders were collected from other colonies within approximately 200 m of our observation colonies. Immigrant spiders were kept together in their respective colonies under laboratory conditions until experimental introduction 6-11weeks after collection (for laboratory husbandry, see Yip et al. 2009). There were 3 types of experimental introductions:

1) To examine how immigrant size/age influences interactions with resident spiders, we introduced 20 paired spiders of two sizes. Pairs consisted of one unsexed juvenile spider and one larger subadult. Eighteen subadults were female, and two were male. Previous laboratory studies (Beavis et al. 2007; Yip et al. 2009) have shown older spiders are more likely to be attacked by the resident adult female. Because any attack would likely disrupt the colony (e.g. a large running spider can cause smaller spiders to scatter and some to leave the retreat), the

two spiders were introduced sequentially. The small juvenile was introduced first. Then the trial was repeated using the subadult, usually the same night, at least one hour later. However, in six cases the subadult escaped while attempting to introduce it to a foreign colony, and the introduction was not completed until 1-2 days later. Although this method confounds spider size and introduction order, previous studies show aggression toward larger spiders without prior exposure to foreign cues (Beavis et al. 2007; Yip et al. 2009), so it is unlikely that prior exposure to unfamiliar juveniles is responsible for subsequent aggression toward subadults (see Results).

2) To examine the response of residents to immigrant adult males, we introduced 13 adult males into foreign colonies.
3) To examine how nestmate status influences interactions, we performed 13 paired introductions, with one spider collected from the colony as it left the retreat (control spider) and one spider of approximately the same age (within one instar) and sex (provided the spider was old enough to be sexed) taken from a foreign colony (immigrant spider). Because subadults were relatively rare, all but one of these paired introductions were done with juveniles (sixth instar and younger). Immigrant and control spiders were introduced in quick succession (as close to simultaneously as possible) in a random order.

We marked immigrant spiders with small dabs of white Testors enamel paint on the carapace and sternum to differentiate them from similarly sized residents. Control spiders in immigrant/control trials were similarly marked. In all introduction experiments, spiders were observed for 1 h or until a spider was attacked and/or killed. Contacts

among individuals were categorized as aggregations (continuous contact for > 1 min), investigative tapping (rapid tapping by the front legs on another spider), face-offs (spiders meeting prosoma to prosoma, with legs intertwined, sometimes with tapping and circling), and attacking (biting, lunging, threatening with open chelicerae) (sensu Yip et al. 2009). We compared attacks/killing between large and small spiders using McNemar tests for matched pair categorical data (Morrison 2010). We compared aggression toward immigrants between colonies with and without subadult and adult male residents using likelihood ratio chi-square tests (also known as G^2 tests). We compared frequency of contact (count data) initiated and received by immigrant and control spiders using Wilcoxon Signed-Rank tests (matched pairs), as these spiders were the same size and introduced simultaneously and therefore any behavioural differences would be the result of colony origin and stochastic interactions. Analyses were conducted in JMP (SAS Institute). Introductions were conducted from February to April of 2007 and March to April of 2008. Not all 22 colonies were available for all three introductions, and each type of introduction was only performed once on a given colony.

Allozyme analysis

We collected 19 colonies (18 included an adult female) and 39 solitary adult females from 14 February to 30 March 2006 from 4 sites in Australia: Mt. Ainslie, Canberra; Bruce, Canberra; Wartook Valley, Victoria; and near Gulargambone, New South Wales. None of these colonies were used in our observational studies or manipulated in any way prior to collection. One third leg was removed and immediately frozen for later analysis from all adult females (n=57). We also sampled a subset of each age-cohort (3-10 spiders) from each colony (n=152). We collected tissue from spiders fifth instar and

older by removing one third leg, as with adult females. Third and fourth instar juveniles were frozen whole, with their entire bodies (excluding abdomen) used for analysis (n=26 of the 152). A control colony of known maternity, consisting of an adult female collected from Mt. Ainslie and 9 of her laboratory-born offspring, was also sampled.

Allozyme electrophoresis was carried out using the Titan III cellulose acetate gel system (Helena Laboratories), with buffers and stains as per Hebert and Beaton (1989). Fourteen allozyme systems previously shown to be variable in *D. cancerides* (Rowell 1990) were assayed. Of these, five were both variable and reliably scored for the populations studied (G6PDH, GPI, IDH, MPI, PGM; for full allozyme names and enzyme commission numbers, see Supporting information, Table S1). Samples were placed on ice in 1.5 ml Eppendorf tubes and crushed in 0.5-1 ml of de-ionized water, depending on the size of the sample. Two to five microlitres of sample were then applied to the gels depending sample strength. Gels were run at 3 mA per gel. GPI, PGM, MPI, and IDH were run with Tris glycine buffer, and G6PDH was run on Tris citrate buffer (Hebert & Beaton 1989).

Allozyme profiles of immature spiders (and some adult males that might be adult sons) were compared to their putative mothers and to each other to establish maternity and the minimum number of males required to produce the diversity of alleles present in each colony. Given the variation in alleles present in each of the four populations (separated by a minimum of 9 km) and the genotype of the adult female, we calculated the probability of detecting a migrant with a genotype taken randomly from the population allele pool.

Pr(detecting migrant) = Pr(G6PDH) U Pr(GPI) U Pr(IDH) U Pr(MPI) U Pr(PGM)

where Pr(allozyme name) is the probability that neither of two alleles combining randomly in proportion to their population frequency are shared by the colony's adult female for that particular allozyme. We assume that each allozyme system is independent so that Pr(detecting migrant) is then the sum of all Pr(allozyme name) minus all of their intersections. We note that these probabilities only apply to migrants originating from the sampled population. The probability of detecting immigrants from outside the sampled population is unknown.

Pair-wise relatedness was calculated using MER v3.0 (sensu Wang 2002). Population allele frequencies were calculated separately for each collection site using all spiders (adults and offspring) sampled at each site. Pair-wise comparisons were then averaged within colonies to find the average within-colony relatedness.

Results

Movement of marked spiders

We tracked the movements of marked spiders among 14 windowed retreats over time to determine which individuals moved into neighbouring retreats and whether these individuals could remain in foreign colonies for multiple days. Eight of these colonies remained viable for the duration of the observation period. Three colonies with offspring (A64, A77, and A81) and all three single females (A72a, A73, and A87) completely abandoned their retreats within three days of being returned to the field (Fig. 1). Over the course of the observations, 37 subadults dispersed from five natal colonies but were never observed in neighbouring colonies. Only spiders of sixth instar and younger (n = 22 spiders) were observed to successfully move into other colonies. Of these 22

juveniles, 12 originated from two colonies that successfully reestablished (A82 and A83), and 10 originated from two abandoned colonies (A64 and A81) (Fig. 1). We observed 7 (32%) of these juveniles in foreign colonies on multiple nights, for 2-32 days (mean days = 12.7 ± 5.1 S.E). No spider was observed in more than one foreign colony. Because spiders moulted off their identifying marks over time, the observed durations that spiders occupied foreign colonies represent minimums and suggest that young spiders are capable of integrating into foreign colonies, rather than just ephemeral vagrancy.

Additional movements included the A81 adult female that moved under bark on two trees without modified retreats. On the second of these trees, the female sealed the edges of the bark with silk, which is typical behaviour of an adult female founding a permanent retreat prior to egg laying. None of her offspring dispersed with her. The A72a adult female was found above the A64 retreat under a loose piece of bark for one night.

Immigrant introductions

We introduced juvenile/subadult pairs, adult males, and immigrant/control pairs into colonies to record the behaviour of resident spiders toward different types of immigrants. Across all three types of introductions, only adult females and juveniles attacked immigrants while subadults ignored them (Fig. 2). Generally, immigrant juveniles were safe in foreign colonies, though they were subjected to increased investigative tapping (Fig. 3). In contrast, subadult and adult male immigrants were frequently attacked and often killed by the adult female. However, the adult female was generally less aggressive toward immigrant subadults and adult males if she had older

offspring of her own. The behaviour of spiders in nest boxes was consistent with this pattern. All three nest box colonies contained juveniles, but none contained subadult or adult offspring. These adult females attacked introduced males and subadults but ignored juveniles. Immigrants in immigrant/controls trials received more investigative tapping in one trial. Both immigrant and control spiders were treated similarly in the remaining two nest box trials. Because of these consistencies, nest box data were pooled with windowed retreat data for further analyses.

In comparing responses to subadult/juvenile pairs in 20 trials, the resident adult female was only aggressive toward subadults (McNemar's test, 14/14 attacks solely on subadults, $\chi 2 = 14$, $p <= 0.0002$; Fig. 2). The 14 attacks included attacks on the two subadult males. In 6 trials, the adult female attacked neither the small juvenile nor the larger subadult. In five of these, the adult female had subadult offspring present during the introduction or subadult offspring that had recently dispersed. In two trials, the adult females attacked the introduced subadults even though the adult females had subadult offspring of their own. Despite these two trials, there was a significant association between the age of the adult female's offspring (defined as either subadult or juvenile) and whether she attacked an introduced subadult (Likelihood ratio chi-square test, $n = 20$, $df = 1$, $\chi 2 = 9.0$, $p = 0.0027$).

A similar pattern was observed for the 13 adult male introductions. Adult females with cohabiting adult males, either present or recently present (n = five trials), were less likely to attack introduced males (Likelihood ratio chi-square test, $n = 13$, $df = 1$, $\chi 2 = 6.29$, $p = 0.0121$).

In contrast to the adult female, resident juveniles tended to be more investigative than aggressive. Juveniles attacked immigrants in 6 of 20 (30%) subadult/juvenile paired introductions (Fig. 2). Attacks by juveniles were light bites that did not appear to cause any serious damage or bleeding. Immigrant juvenile and subadult spiders were equally likely to be attacked by resident juveniles (McNemar's test: 3/6 attacks solely on subadults, 2/6 attacks solely on juveniles, 1/6 attacks on both, $\chi 2 = 0.2$ $p = 0.65$). Juveniles were never observed to attack adult males. Juveniles often inspected introduced spiders with repeated tapping in 84% of subadult/juvenile trials. Juveniles also occasionally engaged in face-offs (face to face contact with entwined legs) with other juveniles (5/20 trials 25%), but never with subadults or adult males. In one case, the face-off preceded an attack by the resident on the immigrant.

In immigrant/control trials, the immigrants were treated differently from the controls (Fig. 3). When all forms of received contact are summed, immigrants received more contact from residents than controls (Wilcoxon sign rank: $z = 22.5$, $p = 0.022$). Immigrants received more investigative taps than controls (Wilcoxon sign rank: $z = 20.0$, $p = 0.02$). There were no differences between the immigrant and the control for any other form of contact, regardless of whether the contact was initiated, received, or in total (Fig. 3). Biting was rare (22 events confined to three trials). All biting events were directed against the immigrant, but, because biting only occurred in three trials, it cannot be statistically tested with trial as the replicate.

Allozyme analysis

Of the 14 allozyme systems analysed, only five provided information useful to assess relationships within colonies. Two alleles were detected for G6PDH, three each for GPI,

IDH and PGM, and seven alleles for MPI (for allele frequencies within populations and relative allele distances, see Supporting information, Table S1).

Fifteen spiders, with alleles incompatible with the hypothesis that they were offspring of the resident adult female, were found in nine of nineteen colonies (47%) (Table 1). All immigrants but an adult male and an eighth instar female were too young to be sexed. Out of 18 colonies with adult females, six had offspring that may have come from multiple fathers (Table 2). One colony, B2, lacked an adult female when collected; however, the alleles of the spiderlings were consistent with a single mother. The colony GB15 was unusual in that 3 adult females were collected from the same retreat. We had assumed that the oldest female (AF1) was the mother of all offspring, but this is unlikely given that she is heterozygous for PGM, while all putative offspring were homozygous (Table 1). Neither alternative female could be the mother of all the offspring either. Regardless of the mother's identity, the spider with the MPI alleles CE was unlike the rest of the immature spiders in the colony in lacking the D allele, suggesting that this spider did not share one or both parents with the other immature spiders (Table 1). The probability of detecting immigrants varied considerably depending on the rarity of the adult female's genotype and region (Table 2). The low probability of detecting immigrants for some colonies indicates that the immigration detected here is an underestimate.

The mean pairwise relatedness within colonies was 0.27± 0.09 SE, where each colony was weighted by the number of spiders analysed. This was both significantly below the 0.5 expected for full siblings (one-sample t test: $t = -2.42$, $df = 18$, $p = 0.026$) and above the 0 expected from a random association (one-sample t test: $t = 2.93$, df =

18, p = 0.009). Colonies with detected immigrants had a mean relatedness of -0.006 ± 0.13 SE, while colonies without had an average relatedness of 0.50 ± 0.08 SE.

Discussion

We studied the inter-colony movement of *D. cancerides* to determine whether spiders actively change and regulate group membership. We found that immigration does occur. Young spiders can immigrate and remain in foreign colonies for long periods, but whether or not older spiders are excluded from the colony depends on the age of the current residents. Immigration significantly depressed within group relatedness below the 0.5 expected for full siblings. We currently lack data on the fitness consequences of this immigration in *D. cancerides*; however, previous research on the costs and benefits of group living in this species, and how these change as both spiders and colonies develop, broadly agree with the patterns of immigration and exclusion found here, suggesting that these patterns of immigration and aggression are adaptive.

We found that immigration occurred in both natural and manipulated colonies. Spiders from colonies that failed to reestablish dispersed and were able to integrate into other colonies. The failure of colonies under natural conditions must occur regularly (e.g. if the bark falls off the tree, the dead tree with the retreat falls down, or if the mother dies when offspring are young), with similar consequences. Despite our manipulations increasing the rate of immigration, our allozyme data confirm the findings of Rowell and Avilés (1995) who detected immigrants in the absence of colony manipulation. Because of fairly low probabilities of detecting migrants by allozyme electrophoresis at some sites (Table 2), the number of immigrants detected here is

undoubtedly an underestimate. Occasional emigration of immature individuals and their acceptance into foreign colonies is likely the norm for this species.

We note that immigrant spiders in our introduced experiments were housed in the laboratory, and artificial conditions could alter recognition cues mediating aggression. However, since juveniles, subadults and adult males were held under the same conditions, methodological artefacts cannot explain differences in aggression among these groups. Further, the aggression by adult females against larger immigrants is consistent both with our marked spiders experiment in the field and with previous laboratory research (Rowell & Avilés 1995; Beavis et al. 2007; Yip et al. 2009). Changes in recognition cues due to laboratory husbandry might have influenced differences between the immigrant and control pairs. However, similar results were previously found in all laboratory spiders, suggesting that field conditions are not necessary for recognition (Yip et al. 2009).

Whether a spider migrates into a foreign colony is a joint decision by both the immigrant and the host colony and depends on the age of the immigrant and the resident offspring. The pattern of immigration is a likely consequence of the benefits and costs of group living (Higashi & Yamaura 1993) and how these change with ontogeny.

Several lines of evidence suggest that young spiders, in particular, benefit from the presence of other spiders. The adult female shares about 50% of the prey she captures in the retreat with young juveniles but not with subadults (Yip & Rayor 2011). Juveniles also occasionally share prey with older siblings and are heavier on average in the presence of older siblings while older subadults receive no benefit from younger

siblings (Yip & Rayor, in review, see Chapter 4). The adult female protects her brood from predators, and smaller, and therefore more vulnerable, spiders should benefit the most from this protection (Yip & Rayor 2011). Finally, spiders younger than the seventh instar are never found solitarily (Rayor et al. in prep.). Thus, younger immigrants benefit directly by obtaining food and protection from other spiders and may survive better by attempting to integrate into foreign colonies than by attempting to live solitarily. Subadults, on the other hand, do not gain food from the adult female or from younger spiders, and improved protection from predators may not be enough to outweigh the risks of entering a foreign colony.

From the colony's perspective, the tolerance of smaller immigrants by adult females may be a consequence of low intra-colony competition. Competition for prey within the webs of the other social spiders is thought to be acute (Ward 1986; Seibt & Wickler 1988, Rypstra 1993). In *D. cancerides*, some prey is captured within the retreat or returned to it, and therefore subjected to competition among nestmates; however, spiders usually forage away from the retreat and capture and consume most prey individually (Yip & Rayor 2011). With relatively little prey competition, the addition of another juvenile to the colony may have little fitness cost to the resident adult female or her offspring, and this cost may fail to justify the cost of evicting the immigrant, especially given the risk of recognition errors (Sherman et al. 1997).

Subadults, on the other hand, were rarely tolerated by unrelated adult females and were never observed to enter foreign colonies, which corroborates previous studies showing increased aggression toward older spiders in the laboratory (Beavis et al. 2007; Yip et al. 2009). Accepting unrelated subadults may be more costly to an adult

female than accepting unrelated juveniles. Unrelated subadults, by virtue of their size, may be a greater threat to younger spiderlings in the colony, and, in the laboratory, older spiders are generally more aggressive (Yip et al. 2009) and may cannibalize unrelated, smaller spiders (Beavis et al. 2007). Additionally, female subadults could mature before the resident female's offspring, inherit the retreat and threaten the matrilineal line. Immigrants smaller than the adult female's offspring would be more likely to mature after her offspring and therefore pose less risk of inheritance. This hypothesis is supported by our data showing that larger immigrants were safer in colonies in which the adult female had offspring of similar size or larger. An alternate hypothesis is that the adult female is simply incapable of differentiating between an immigrant and her own offspring of similar size. Some spiders reduce predatory behaviour after producing offspring (Moring & Stewart 1992; Wagner 1995). However, young *D. cancerides* spiders are capable of differentiating unfamiliar (and unrelated) spiders from nestmates (Rowell & Avilés 1995; Beavis et al. 2007; Yip et al. 2009), suggesting there are no barriers to the evolution of kin recognition, should natural selection favour it.

A consequence of this exclusion is that dispersing subadults must search for unoccupied retreats, rather than join established colonies. Habitat saturation is common. At about half of collection sites, 90-100% of suitable retreats are already occupied by colonies (Rayor et al. in prep.). The need to locate free retreats in saturated habitats may force subadults or newly mature spiders to disperse longer distances than juveniles and therefore suffer greater dispersal costs. Under the ecological constraints hypothesis (Emlen 1982) this may in turn lead to subadults

persisting in the natal retreat to either inherit the retreat or to delay dispersal until they are larger and more likely to successfully compete for other retreats.

The presence of immigrants correlated with depressed relatedness below the 0.5 expected for full siblings, suggesting that immigration may alter the fitness consequences of group interactions. Low relatedness could impede the evolution of cooperative behaviours according to kin selection theory (Hamilton 1964). In other social spiders, kin groups are more efficient in feeding than non-kin (Schneider & Bilde 2008; Ruch et al. 2009) and build larger webs than non-kin (Evans 1999). In *D. cancerides*, however, there was no effect of relatedness on the extent of prey sharing among similarly-sized spiders (Auletta & Rayor 2011). Given the importance of older siblings to the condition of young spiders (Yip & Rayor, in review, see Chapter 4), it would be interesting to investigate whether relatedness influences prey sharing among spiders with size and dominance asymmetries. Decreased relatedness is also known to provide a variety of benefits in the social hymenoptera (Crozier & Fjerdingstad 2001), such as greater resistance to pathogens (i.e. Baer & Schmid-Hempel 1999), although this has not been tested in any social spiders. The variability of within group relatedness reported here for *D. cancerides* suggests that this may be an excellent model system to test the importance of kin selection and kin recognition on group living and whether lowered relatedness presents a benefit or a cost.

Whether relatedness within *D. cancerides* colonies is particularly low or whether inter-colony migration is particularly high compared to other social spiders is difficult to assess because directly comparable data are few. In the cooperative spiders that forgo dispersal every generation and instead form inbred lineages, there is strong evidence

that inter-colony migration is rare or virtually absent (Avilés 1997; Lubin & Bilde 2007; Johannesen et al. 2009; Agnarsson et al. 2010). However, migration among family groups in the subsocial spiders is far less studied. Johannesen et al. (1998) and Johannesen and Lubin (2001) examined allozymes in two species of subsocial eresids and both found relatedness among separate nests to be about the 0.25 expected for half siblings. However, they only examined relatedness among neighbouring nests after natal dispersal and not within a single nest with one putative mother, as examined here. Presumably the relatedness among spiders within a single nest prior to dispersal would be closer to the 0.5 expected for full siblings. Similarly in *Anelosimus studiosus*, Duncan et al. (2010) calculated relatedness among clusters of solitary breeding nests and among adult females in communally breeding nests, but not among offspring within a single nest. Relatedness among *A. studiosus* adult females in communal nests was about 0.25 (Duncan et al. 2010). The only species for which there are comparable data is the thomisid *Diaea ergandros* (Evans & Goodisman 2002). Evans and Goodisman (2002) reported an average relatedness of 0.44 within single family groups and that 3.5% of sampled nests had migrants; however, for greater migration in a smaller sample than that of Evans & Goodisman (2002) see Evans (1998). The average relatedness of 0.27 found within colonies of *D. cancerides* may be relatively low considering that other studies found a similar relatedness post natal dispersal.

Patterns of movement among colonies align with previous research suggesting that young spiders benefit from living in groups more than older spiders and that older immigrants are a greater threat to residents. This suggests that social groups are not always the passive result of delayed dispersal, but rather that some individuals seek to

join other colonies while some colonies may exclude some individuals. Such active grouping shares some similarities with the fission-fusion societies of mammals (Chapmen et al. 1995; Smith et al. 2008) or drifting in bees (Beekman & Oldroyd 2008). However, one key difference is that *D. cancerides* immigrants are exclusively juveniles. This system is perhaps most similar to parental care in some fish, where fry can move among groups (Wisenden 1999). The Central American convict cichlid (*Cichlasoma nigrofasciatum*) even excludes immigrant fry larger than its current offspring, similar to our results here (Wisenden, 1999). The patterns of movement presented here for *D. cancerides* set a baseline of data for further inquiry into the role of inter-colony movements on the evolution of group living and social behaviour.

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Table 1

Instar	G6PDH	GPI	IDH	MPI	PGM
Colony A22					
AF	AA	AB	AB	AC	AB
6th-8th	AA	BB	AB	AC	BB
6th-8th	AA	AB	AA	AA	AC
6th-8th	AA	BB	AA	AA	AB
6th-8th	AA	AB	AB	AA	BB
6th-8th	AA	AB	BB	CD	AC
5th	AA	AB	?	CE	BB
5th	AA	AB	AA	CE	BB
5th	AA	BB	AB	**BB**	AB
4th-5th	AA	AA	BB	BC	BB
4th-5th	AA	BB	BB	AB	BC
Colony B4					
AF	AA	BB	BB	AB	BB
5th-7th	AA	BB	BB	AB	BB
5th-7th	AA	BB	?	AA	BB
5th-7th	AA	BB	BB	AB	BB
5th-7th	AA	BB	BB	AB	BB
5th-7th	AA	BB	BB	AB	BB
5th-7th	AA	BB	BB	AB	BB
5th-7th	AA	BB	BB	AB	BB
5th-7th	AA	BB	BB	AA	BB
5th-7th	AA	BB	AB	**DG**	BB
5th-7th	AA	BB	BB	AB	BB
5th-7th	AA	BB	BB	AB	BB
Colony GB15					
AF1	AA	BB	BB	DD	**AB**
AF2	AA	BB	BB	**EF**	BB
AF3	AA	**AB**	BB	DD	BB
6th	AA	BB	BB	DD	BB
6th	AA	BB	BB	DD	BB
6th-8th	AA	BB	BB	CD	BB
6th-8th	AA	BB	BB	**CE**	BB
6th-8th	AA	BB	BB	DD	BB
6th-8th	AA	BB	BB	CD	BB
6th-8th	AA	BB	BB	DD	BB
6th-8th	AA	BB	BB	DE	BB
AM	AA	BB	BB	DD	BB
AM	AA	BB	BB	DD	BB
Colony GB9					
AF	AA	BB	BB	DE	BB
5th	AA	BB	BB	**CC**	BB
5th	AA	BB	BB	CD	BB
5th	AA	BB	BB	DE	BB

Instar	G6PDH	GPI	IDH	MPI	PGM
Colony A5-1					
AF	AA	AB	BB	CD	BB
AM	AA	AB	BB	CC	BB
AM	AA	AA	AB	CD	BB
AM	AA	AB	BB	BD	BC
AM	AA	BB	**AA**	CC	BC
AM	AA	AA	AB	CC	BB
8th	AA	BB	**AC**	CD	BB
8th	AA	AB	BB	CD	BB
8th	AA	AA	BB	CD	BB
5th	AA	AB	AB	**BB**	BB
AM	AA	AA	BB	CD	BB
Colony G7					
AF	AA	BB	BB	CD	AB
7th	AA	BB	BB	CD	AB
7th	AA	BB	BB	CD	BB
7th	AA	BB	BB	CD	AB
7th	AA	BB	BB	CD	AB
7th	AA	BB	BB	CD	AB
7th	AA	BB	BB	CD	AB
3rd	**BB**	BB	BB	CC	AB
3rd	**BB**	BB	BC	CC	AB
3rd	AB	BB	BB	CC	AA
3rd	AA	BB	BB	CC	AA
Colony A25					
AF	AA	AA	BB	BD	BB
3rd	**BB**	AB	AB	BB	AB
3rd	**BB**	AB	AB	**AA**	AB
3rd	**BB**	AB	BB	**AA**	AB
3rd	AB	AA	BB	BC	BB
Colony B12					
AF	AA	AB	*	CD	BB
3rd	AB	AB	AA	BC	AB
3rd	AB	AB	AB	BC	AB
3rd	AB	AB	AB	**AB**	AB
3rd	AB	AB	AA	AD	AB
Colony GO1					
AF	AA	BB	BB	AC	BC
3rd	AA	BB	BB	AC	AB
3rd	AA	AB	BB	AA	**AA**
3rd	AB	BB	AB	AA	**AA**

Table 1. All colonies that contained migrants and their analyzed spiders. The instar of the migrant and its alleles that were incompatible with the hypothesis that the adult female is its mother are in **bold**. 'AF' stands for adult female, and 'AM' stands for adult male. The alleles of the three GB15 adult females indicating that each is probably not the mother of all offspring are also in **bold**. '?' indicate that this allozyme stained too weakly to be reliably read for this spider. * This female stained weakly for IDH, but her genotype was either AA or AB, either being compatible with non-excluded offspring.

Colony	Population	Alleles Supplied by the Father(s)					Min. Number of Fathers	Probability of Detecting Migrants	r	Migrants Detected?
		G6PDH	GPI	IDH	MPI	PGM				
A1	Mt. Ainslie	A	A, B	B	B	B, C	1	0.39	0.62	No
A5-1	Mt. Ainslie	A	A, B	A, B	C	B, C	1	0.41	0.22	Yes
A5-2	Mt. Ainslie	A	A, B	B	B, C	B	1	0.47	0.78	No
A22	Mt. Ainslie	A	A, B	A, B	**A, B, D, E**	B, C	2	0.35	-0.25	Yes
A25	Mt. Ainslie	B	A	B	C	B	1	0.56	-0.30	Yes
B2	Bruce							NA	0.18	No
B4	Bruce	A	B	B	A	A	1	0.72	0.67	Yes
B6	Bruce	A	B, C	B	B, E	B	1	0.19	0.46	No
B8	Bruce	A	A, B	A, B	**C, B, E**	B	2	0.63	0.43	No
B11	Bruce	A	A, B	B	B, E	B	1	0.57	0.43	No
B12	Bruce	B	A, B	A, B	A, B	A	1	0.62	0.11	Yes
B13	Bruce	A	B	B, C	**A, B, C**	B	2	0.15	0.42	No
B16	Bruce	A	A, B	A, B	**A, B, E**	A, B	2	0.19	0.46	No
GO1	Bruce	A	B	B	A or C	A	1	0.38	0.15	Yes
G1	Grampians	A	B	B	D	B	1	0.32	1	No
G7	Grampians	A	B	B	C	A, B	1	0.03	0.12	Yes
GB9	Gulargambone	A	B	B	C, D or E	B	1	0.03	-0.41	Yes
GB15	Gulargambone							NA	-0.45	Yes
GB18c	Gulargambone	A	B	B	**C, D, E**	B	2	0.07	0.24	No
Control	Mt. Ainslie	A	A	A	C	C	1	NA	0.62	No

Table 2. Summary of allozyme data for all colonies, showing the detection of migrants and multiple fathers and the probability of detecting migrants. Alleles that must have been supplied by more than one sire are in **bold**. 'r' is relatedness. Colonies B2 and GB15 lacked a clear mother and were therefore not analysed for the presence of multiple fathers or the probability of detecting migrants. The 'Control' colony consisted of spiders born in the laboratory, without the possibility of immigration.

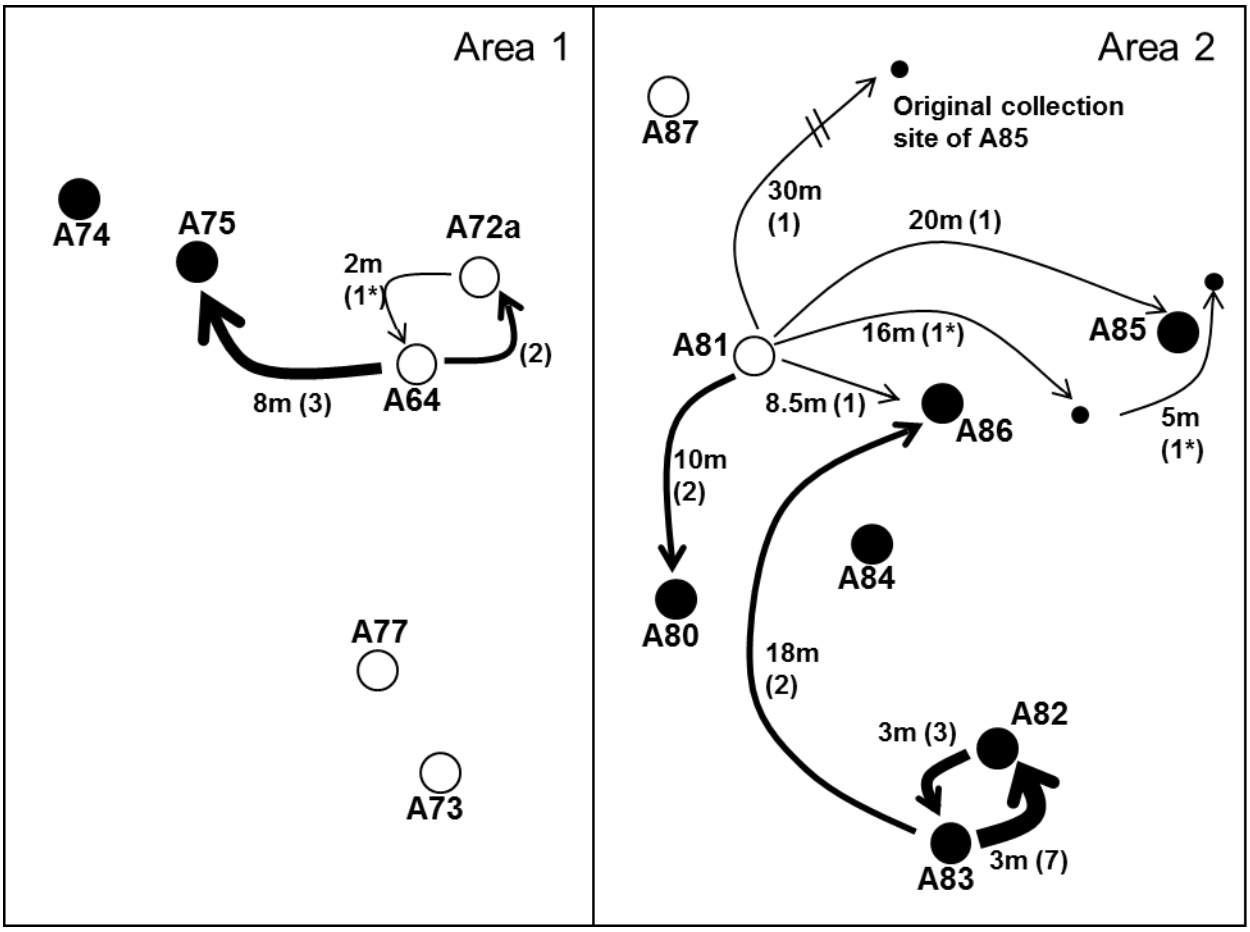

Figure 1. The spatial relationship of marked spiders and their movement among colonies. Open circles indicate colonies that were abandoned during observations. Large black circles indicate colonies that reestablished and persisted for the duration of the observations and beyond. Small black circles indicate other trees in the area on which spiders were found and also the original collection site of A85 that was then moved to its current position. The arrows indicate movements of spiders, and their thickness indicates the relative numbers of spiders, with the exact numbers indicated in parentheses. An asterisk indicates movement of the adult female.

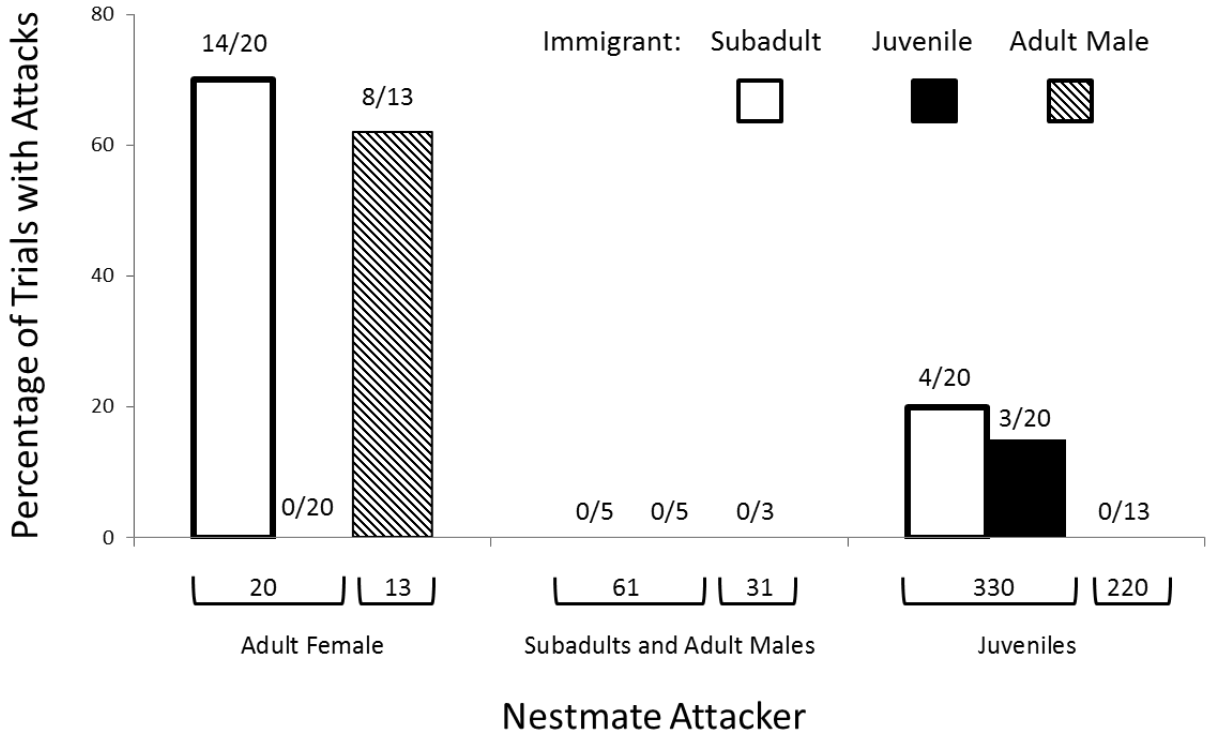

Figure 2. Aggression by colony members against introduced immigrant spiders, measured as the percentage of trials with attacks. Both juvenile/subadult pairs (grouped by parenthesis) and adult male trials (separate parenthesis) are included but not immigrant/control paired trials (Fig. 3). Numbers inside parentheses indicate the total number of spiders of that age group summed over all trials. Numbers over bars indicate the number of trials with aggression over the total number of trials. Note that not all trials used colonies containing subadults or adult males, so the trial number for these data is lower. Note that, in two juvenile/subadult and two adult male trials, subadult and adult male nestmates had recently dispersed but were not present during the introduction.

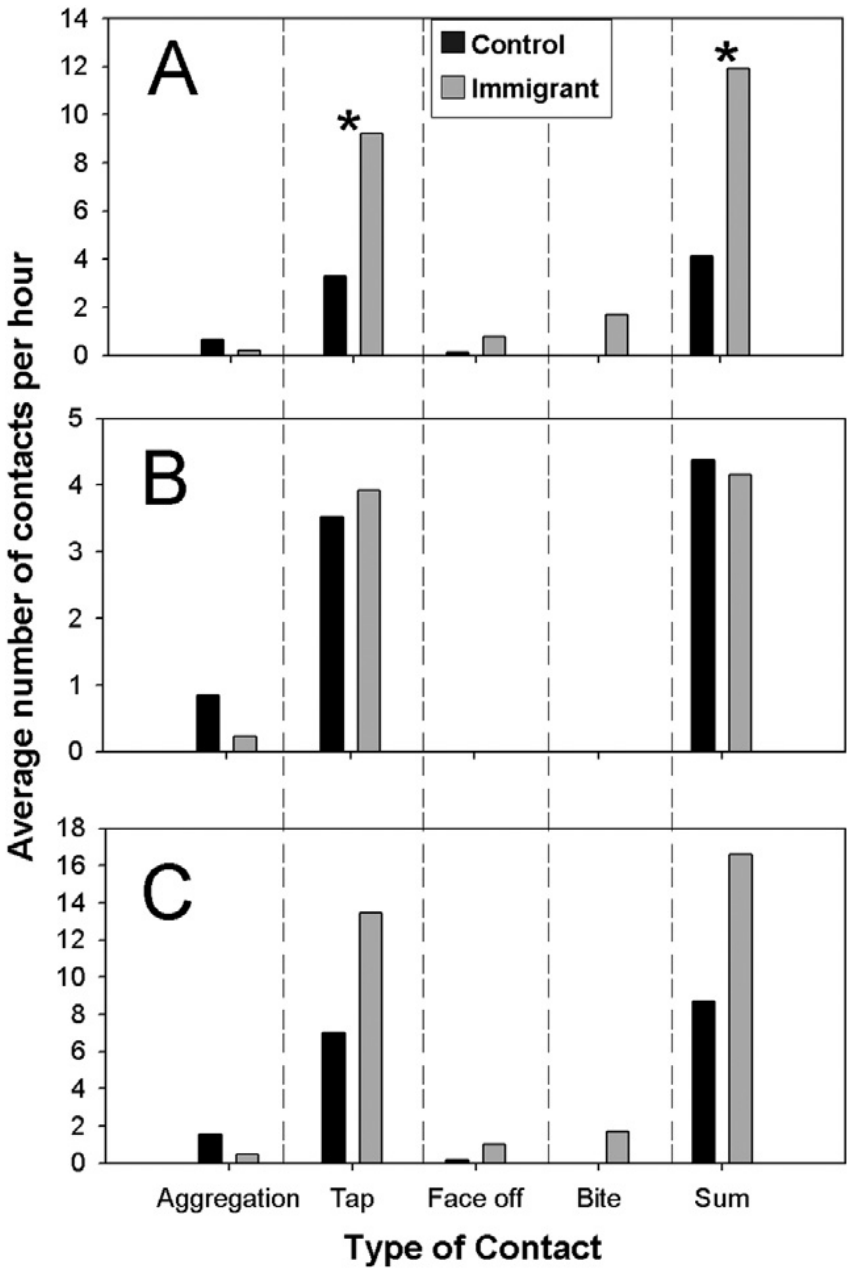

Figure 3. The number of contacts for the control and immigrant that were matched for size and sex and introduced simultaneously in 13 trials. Contacts are divided by type and by A) received contact, B) initiated contact, and C) summed received, initiated, and mutually initiated contact. An (*) indicates significant differences between immigrant and control.

Supporting information

Table S1

Full Name	Abbreviation	EC #	Alleles	Relative Allele Distances	Ainslie Frequency	Bruce Frequency	Grampians Frequency	Gulargambone Frequency
Glucose-6-phosphate Dehydrogenase	G6PDH	EC 1.1.1.49	A	1	0.95	0.96	0.91	1
			B	1.07	0.05	0.04	0.09	0
Glucose-6-phosphate Isomerase	GPI	EC 5.3.1.9	A	1.15	0.42	0.12	0	0.2
			B	1	0.58	0.86	0.98	0.98
			C	0.65	0	0.02	0.02	0
Isocitrate Dehydrogenase	IDH	EC 1.1.1.42	A	1.06	0.25	0.33	0.05	0
			B	1	0.75	0.64	0.93	1
			C	0.94	0.01	0.03	0.02	0
Mannose-6-phosphate Isomerase	MPI	EC 5.3.1.8	A	1.06	0.11	0.29	0	0
			B	1	0.43	0.36	0	0
			C	0.91	0.34	0.22	0.33	0.13
			D	0.85	0.11	0.03	0.59	0.73
			E	0.75	0.01	0.09	0.09	0.12
			F	0.58	0	0.01	0	0.02
			G	1.19	0	0.01	0	0
Phosphoglucomutase	PGM	EC 5.4.2.2	A	1.4	0.1	0.2	0.21	0.02
			B	1	0.7	0.78	0.74	0.98
			C	0.65	.2	0.01	0.05	0

Summary information for each allozyme system, including the allozyme's full name, enzyme commission number (EC #), the relative frequencies of each allele at each collection site, and the relative distances each allele traveled through the gel. The most common allele was designated with a distance of 1, with all other alleles measured relative to this distance.

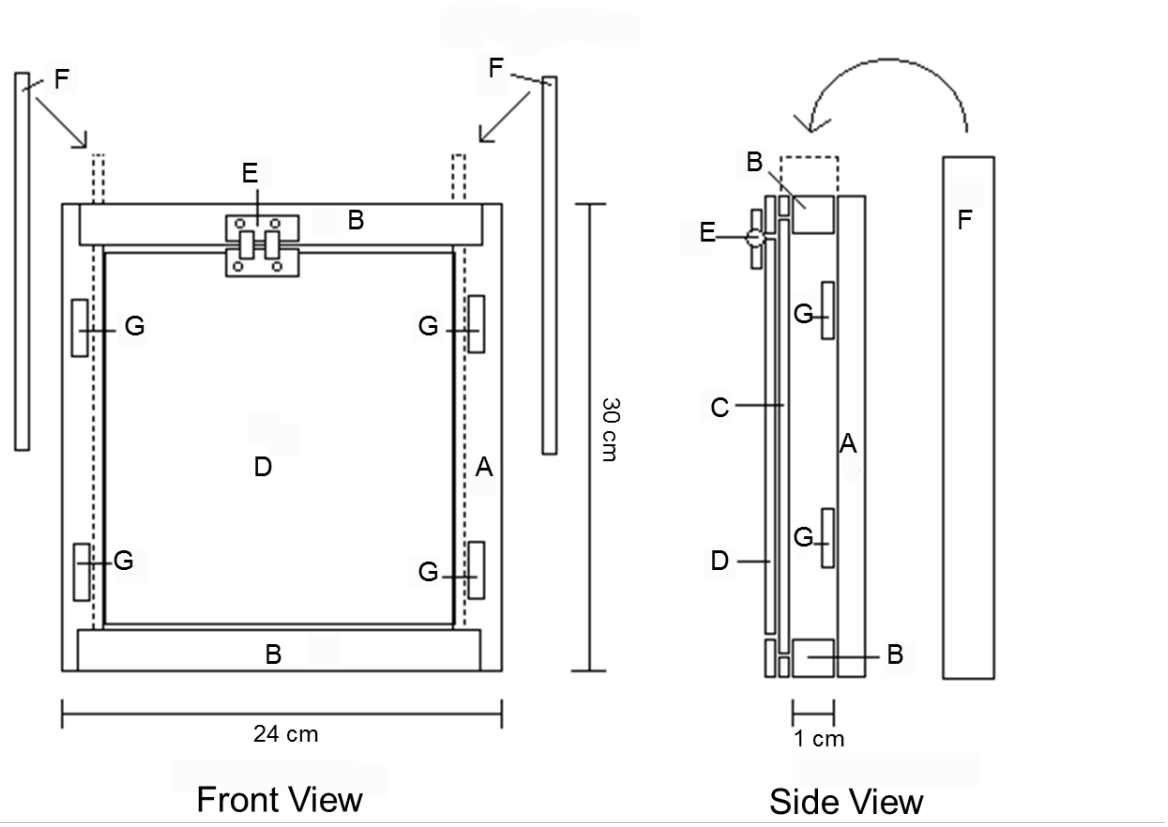

Figure S1. The structure of nest boxes. The box was constructed with a ¼ in (0.635 cm) plywood back (A). Three pieces of wood were glued to form a top and base with a groove (B). A clear acrylic sheet (C) fit into the groove. The acrylic was covered by a wood cover (D), attached to the top by a hinge (E). Removable sides (F) sealed the treat (movement indicated by arrows and dashed lines), and these were held in place by 4 blocks (G). One side (F) was removed at the time the nest box was placed in the field, allowing the spiders to enter and exit the nest box freely.

CHAPTER 4

The influence of siblings on body condition in a social spider: Is prey sharing cooperation or competition?

E.C. Yip, L.S. Rayor

Abstract. Siblings raised together must compete with each other for resources, yet they may also cooperate to maximize their inclusive fitness. In social spiders, siblings share prey and may both compete and cooperate to obtain this resource. In the laboratory, the social huntsman spider, *Delena cancerides*, will readily share prey captured by other colony members; however, these spiders only occasionally share prey in the field, making the importance of prey sharing to their social system difficult to assess directly. We examined the importance of prey sharing indirectly by measuring the condition of spiders from 90 colonies at the time of collection. We compared body condition to colony demographics to determine whether the patterns were consistent with the hypothesis that younger spiders benefit from sharing prey captured by older siblings. We tested several alternative hypotheses that might also explain associations between condition and the presence of siblings. We further conducted a laboratory experiment to determine whether sharing prey with older siblings improves the condition of younger spiders. Younger spiders collected from the field were heavier in the presence of older siblings, but there was no effect for older spiders or for any spider with younger siblings.

Laboratory spiders gained access to additional prey captured by older siblings. We rejected the alternative hypotheses and concluded that younger spiders indeed benefited from the presence of older siblings. This system provides evidence that the exploitation of others' resources can provide a benefit of group living and act as a form of cooperation.

Key Words**:** Competition, Condition, Cooperation, Foraging, Prey Sharing, Producer-Scrounger, Siblings, Sociality, Spiders

Introduction

The clustering of siblings in both time and space sets two forces in opposition to each other: Competition for resources promotes sibling conflict, while relatedness promotes cooperation to maximize inclusive fitness (Mock & Parker 1998). This opposition produces a wide variety of sibling interactions, from siblicide (Mock & Parker 1998; Mackauer & Chau 2001; Heintz & Weber 2011) to alloparental care by siblings (Riedman 1982; Koenig et al. 1992; Hatchwell 2009).

In the subsocial and cooperative spiders ('non-territorial periodic' and 'non-territorial permanent' social, sensu Avilés 1997), offspring remain in the natal nest and compete and cooperate with their siblings. Cooperative foraging is a primary benefit of group living in spiders (Whitehouse & Lubin 2005), and siblings will often cooperate in prey capture, allowing spiders to subdue prey much larger than a single spider could capture (Buskirk 1981; Ward 1986; Jones & Parker 2002). However, competition for prey is also intense (Ward 1986; Seibt & Wickler 1988), and some spiders in the colony

fail to obtain enough resources to reproduce (Avilés & Tufiño 1998; Bilde et al. 2007). In addition, whether an individual is helped or hindered by a sibling may depend on size and age asymmetries. For example, in the social spider, *Anelosimus eximius*, large females will often usurp smaller females' feeding positions rather than capture prey themselves (Ebert 1998). Interactions among siblings over prey are therefore crucial to the costs and benefits of spider sociality, both in determining whether spiders should tolerate siblings and whether mothers should allow older broods to stay with younger cohorts.

The Australian social huntsman spider, *Delena cancerides*, is unusual among social spiders in lacking a prey capture web. Instead, colonies, consisting of a single mother and multiple cohorts of offspring, live under the bark of trees (Rowell & Avilés 1995; Rayor et al. in prep.). Yip and Rayor (2011) investigated the foraging behavior of these spiders, given that they lack a capture web to facilitate cooperative foraging. Spiders predominantly foraged individually away from the bark retreat. Spiders occasionally shared prey captured within the retreat, and spiders foraging outside at dawn occasionally returned to the retreat with prey. Prey remains at the bottom of retreats further suggest that, over time, a considerable amount of prey is consumed inside the retreat where it might be shared (Rayor et al. in prep.). However, overall, shared prey made up a small percentage of the total prey captured by spiders (Yip & Rayor 2011). The rarity of an event, however, does not preclude its importance. For example, in *A. eximius*, very large prey account for only 8% of the number of captured prey, but 75% of the total captured biomass (Yip et al. 2008). Similarly, in orb weaving spiders, large prey items are only 17% of the prey numbers but 85% of consumed

biomass (Blackledge 2011). These relatively rare feeding events are critical for spider fitness. Despite the rarity of prey sharing in *D. cancerides*, these spiders remain in groups even in the absence of the mother, who is the primary benefactor of young spiders (Yip & Rayor 2011), suggesting that young spiders benefit from siblings in ways that are difficult to observe.

Here, we investigated the possibility that, though rare, prey sharing may provide substantial benefits to some spiders within the colony, yet the rarity of prey sharing in the field renders direct observations impractical. Therefore, we adopted an indirect approach, combing field data with a complementary laboratory experiment.

In the field, we recorded a snapshot the 'body condition' of a large number of spiders at the time of collection and examined how condition changed with colony demographics. We hypothesized that younger spiders benefit from sharing prey with older spiders for the following reason: One unusual characteristic of *D. cancerides* social structure is the retention of older cohorts alongside younger cohorts within the colony (see Fig. 1 for instar sizes), and this heterogeneity in individual size should lead to an asymmetry in prey sharing. Predator size positively correlates with prey size, in spiders generally (Buskirk 1981), and also in *D. cancerides* (EC Yip unpubl. data). Therefore, older and larger spiders have access to a greater range of prey and would be expected to capture prey of greater size and more frequently than younger and smaller spiders. This would lead to younger spiders disproportionately benefiting from prey sharing and adopting prey sharing as a 'scrounger' tactic (Giraldeau & Beauchamp 1999; Beauchamp 2006). Small spiders, because of their size and relatively low metabolic rate (Rayor et al. in prep.), likely consume a relatively small portion of large spiders' prey (Auletta & Rayor

2011). This hypothesis yields two predictions: One, younger spiders should be heavier (have a better condition) in the presence of older siblings. Two, older spiders should fare slightly worse or about the same in the presence of younger siblings.

Other hypotheses may also yield one or both of the above two predictions. A prey-rich habitat may promote both the production of multiple egg sacs (i.e. multiple cohorts) and an increase in overall condition, thereby leading to an association between condition and the presence of older siblings. Female fecundity may decrease over time so that younger cohorts have fewer individuals, which may lead to decreased competition within cohorts and therefore improved condition, or older siblings may preferentially cannibalize younger siblings in poor condition. All these alternative hypotheses predict either a reduction in the size of younger cohorts or the overall improved foraging success of the entire colony. Therefore, if younger spiders are truly benefiting from sharing prey with older siblings, two other additional predictions must be satisfied: One, colony size should not correlate positively with spider condition, as this would indicate a prey-rich environment that would promote both the production of multiple cohorts (and greater colony size) and improved condition. Two, young cohorts should contain roughly the same number of individuals, regardless of the presence of older siblings.

In the laboratory, we further tested whether young spiders benefit from sharing prey with older siblings by examining how the presence of older siblings affects the change in body condition following feeding. We distinguished among three competing outcomes: One, older spiders monopolize all or most prey; two, spiders eat what they capture, essentially independent of siblings; or three, older siblings share prey too large

for small spiders to capture with younger siblings. Of these, only the third outcome supports our hypothesis that younger spiders can benefit by sharing prey with older siblings.

Methods

Condition of Spiders in the Field

A total of 90 colonies, containing 2,822 spiders third instar and older, were collected from 25 sites in and around Canberra, Australia and one site near Oberon, New South Wales. An additional 10 adult females that had not yet reproduced were also collected. These females were only included in analyses on the relationship between colony size and average body condition (these data represented colony sizes of one). An additional 329 spiders escaped during collection; they were included only for purposes of calculating total colony size. *Delena cancerides* spiders emerge from the egg sac as second instars and do not feed. Non-feeding second instar spiderlings were not included in our analyses. Entire colonies were collected from March 2006 to March 2010 in all months of the year except during the austral winter (May, June, and July). Spiders were measured immediately after collection, but due to large colony sizes the measurements occasionally took up to 3 days to complete. While measurements were taken, spiders were kept at room temperature without food or water. Spiders were kept in 45 or 120 ml plastic vials with > 4 air holes poked in the top during the measuring process. We weighed spiders to the nearest tenth of a mg and used dial calipers to measure maximal carapace width to the nearest tenth of a mm. We noted whether spiders were missing legs, had recently regenerated smaller legs, were newly molted,

or were approaching a molt. As spiders become darker 1-3 days prior to molting and remain pale for ~24 h afterward, we used the color of the cuticle as an indicator of molt status. Eighteen spiders that died or may have cannibalized other spiders during collection were excluded from calculations involving condition; they were included in colony population size.

We used a modified version of a 'residual index,' in which the condition of an individual is defined as the residual off of the regression of weight and some linear measure of body size (Jakob et al. 1996). This method has been successfully used to estimate body condition for several spider species, using carapace width as a measure of body size because the carapace is heavily sclerotized and does not expand with feeding (Jakob et al. 1996, öberg 2009). We modified the residual index by performing a multiple linear regression that included, in addition to the log transformation of carapace width, sex, number of legs, number of small re-grown legs, molt status, and days until measurement (0-3) as effects predicting the log of spider weight to remove these factors from our measure of condition. The condition of a spider is the residual off its predicted weight. Using mass residuals as a measure of condition has been criticized for lacking power and failing to uncover more complex patterns compared to other measures of condition (Moya-Larano et al. 2008). However, Moya-Larano et al. (2008) also found that, of the measures they tested, only body condition based on mass consistently correlated positively with increased feeding, which is what we seek to uncover. Our data on *D. cancerides* from laboratory feeding regimens confirm that increased food intake results in better condition, as we define it (see Supporting information).

Here, we use mass as a correlate of fitness. Increased body weight has been found to correlate with increased mating success in male spiders and increased fecundity in female spiders (Vollrath 1987). The second deposition of yolk in the eggs is contingent on the adult female having adequate food supplies (Foelix 1996). Our study is primarily concerned with immature spiders for which weight is critical to development and molting time and adult size (Vollrath 1987; Jakob & Dingle 1990; Foelix 1996).

Comparing the Condition of Spiders with and without Siblings

The interval between clutches is typically such that siblings from subsequent clutches are two to three instars apart in development. We designated a given spider as having older or younger siblings if at least one other non-parental spider (i.e. excluding adult females) in the colony was at least two instars larger, in the case of an older sibling, or smaller, in the case of a younger sibling. A two instar difference corresponded to ~2 mm difference in carapace width between juveniles third to sixth instar, and ~4 mm difference in carapace width between older juveniles and subadults sixth to ninth instar (see Fig. 1 for instar sizes).

We examined the correlation between condition and the presence of siblings using a mixed model with colony as a random effect to account for the non-independence of spiders from the same colony. The presence of younger siblings and the presence of older siblings were effects, with the presence of the adult female and season (defined as the ordinal progression of months starting in August, the Austral spring) included as covariates. Instars were analyzed separately. Adult males were not analyzed because it was uncertain whether adult males were adult sons (and therefore

long-term residents of the colony), or whether they were immigrants (Yip et al. 2012). Altogether, 2597 spiders third to ninth instar were included in this analysis.

We used similar mixed models to examine how spider condition correlated with the number of older or younger siblings and the average size difference (measured as carapace width) between a given spider and its older or younger siblings. Spiders without older or younger siblings were excluded from these analyses. As with the analysis on presence/absence of siblings, we included the presence of the adult female and season as covariates and colony as a random effect. Unlike our analysis on the presence/absence of siblings on condition, we could not examine younger and older siblings simultaneously because relatively few spiders had both older and younger siblings. We therefore examined the effects of older and younger siblings separately for the purposes of sibling number and average size difference.

Testing Alternative Hypotheses

To determine if condition correlates with total colony size, we examined the regression of mean condition within colonies to colony population size using season as a covariate. To determine whether second cohorts are smaller than first cohorts, we compared the number of third and fourth instars in colonies with one cohort to colonies with multiple cohorts (third and fourth instars are too young to have younger siblings that feed). We compared the number of fifth instars in colonies with one cohort to colonies with multiple cohorts, where colonies in which fifth instars are older siblings are removed from the analysis. Because transformations did not normalize the residuals, we used Wilcoxon (rank sums) tests to compare cohort sizes.

The Effects of Older Siblings on Condition in the Laboratory

We selected 20 laboratory colonies that had multiple cohorts of young. All colonies were descendants of spiders originally collected near Canberra, Australia and kept under laboratory conditions described in Yip et al. (2009). From each colony, we randomly selected three young juveniles (third to fifth instar), although spiders near a molt or that had recently molted were excluded because these spiders typically do not feed. We randomly assigned each spider to one of three treatments: One, solitary feeding; two, feeding with a sibling of the same instar; three feeding with an older sibling (at least two instars larger). Each spider and its sibling (if appropriate) were placed in 7.5x5.5x5.5 cm plastic containers. These containers were small because, in natural retreats, spiders typically rest in contact with each other (Rayor et al. in prep.). We weighed all spiders to the nearest tenth of a mg and measured their carapace to the nearest tenth of a mm. We supplied one prey item that could be captured by the young spider (*Drosophila melanogaster*, house flies, or house cricket nymphs depending on spider size) to each treatment. We attempted to standardize this small prey weight among treatments. In all but six trials, all individual prey weights were within 20% of the mean weight. In the remaining six trials, individual prey weights were within 40% of the mean weight. A post hoc analysis found no difference in prey weight among treatments (Mean prey weight for single spiders = 9.8 mg; for spiders with same instar siblings = 9.3 mg; for spiders with older siblings = 9.8 mg; ANOVA: $F_{2,59} = 0.015$, $p = 0.99$). In addition to these small prey items, one cricket, too large to be captured by the young spider (at least three times the younger spider's mass), was supplied to the treatment with an older sibling that could capture the prey item. All spiders were reweighed 24 h after the introduction of prey. We calculated their condition before and after feeding as

we did for field collected spiders, but we only included carapace width as an effect because no other effect was a significant predictor of variation in our laboratory spiders. We then compared the change in condition among the three treatments using matched-pairs analyses, where treatments were compared within each colony. All statistics were conducted in JMP.

This design allows us to generate predictions distinguishing among our three prey sharing outcomes. One, if older spiders are monopolizing the prey, we predicted that spiders kept with older siblings to have the poorest change in condition. Two, if spiders eat what they capture independent of siblings, we expected the spiders with the older siblings to perform about as well as spiders with siblings of the same size, as spiders in both treatments would have about a 50% chance of capturing the only prey item small enough to capture. Under this hypothesis, we expected the solitary spider to perform the best because it has sole access to the prey item. Three, if spiders share prey captured by their older siblings, spiders with older siblings gain access to two prey items instead of one and therefore should outperform spiders with siblings of the same size. They may also outperform solitary spiders if sharing the large prey item more than compensates for any of the small prey item lost to the older sibling.

Results

Colony demographics

Demographics of the 90 colonies varied from 2-113 spiders. Colony age structure ranged from single females with third instar spiderlings to subadults without an adult. Eight colonies lacked an adult female, and all eight of these colonies contained at least

one subadult. Sixteen colonies had nearly every instar represented (six to seven out of seven feeding instars present). Forty-two colonies consisted of a single cohort of young; 48 colonies had two or more cohorts.

Comparing the Condition of Spiders with and without Siblings

Young spiders (third, fourth, and fifth instar) were heavier in the presence of older siblings (Table 1). There was no correlation between condition and the presence of older siblings for older spiders or the presence of younger siblings for spiders of any age. As the season progressed from spring to winter, spider condition consistently declined, though the difference was not significant in subadults. The presence of the adult female correlated with increased condition in third instars but not in any other instar (Table 1).

Of spiders that did have older or younger siblings, there was no correlation between condition and the number of these siblings for any instar (Table 2). Third instars were heavier as their older siblings increased in size. The difference in size between spiders and their older or younger siblings did not correlate with condition for any other instar (Table 2).

Tests for Alternative Hypotheses

There was no correlation between average condition of a colony and the number of spiders in the colony, although average condition decreased from spring to winter (Multiple linear regression: R^2 adjusted = 0.28, n = 100; Colony Size: t = 0.86, p = 0.39; Season: t = -6.35, p = < 0.0001; Fig 1). Younger cohorts were the same size regardless of the presence of older cohorts. The numbers of third and fourth instars (instars that would only have older and not younger siblings) were similar between colonies with only

one cohort and colonies with multiple cohorts (mean number of third instars single cohort = 17.3 ± 3.8 S.E., multiple cohorts = 16.3 ± 2.8 S.E.; mean number of fourth instars single cohort 10.7 ± 1.9 S.E., multiple cohorts = 6.4 ± 1.6 S.E.; Wilcoxon rank sums test: third instars, $\chi 2 = 0.068$, $n = 45$, $p = 0.79$; fourth instars, $\chi 2 = 0.98$, $n = 57$, $p = 0.32$). The number of fifth instars was also similar between colonies with one and multiple cohorts when colonies in which fifth instars were older siblings were removed (mean number fifth instars single cohort = 9.2 ± 2.0 S.E., multiple cohorts = 10.0 ± 1.8 S.E.; Wilcoxon rank sums test: $\chi 2 = 0.052$, $n = 54$, $p = 0.82$).

The Effects of Older Spiders on Condition in the Laboratory

Our laboratory experiment examined how prey sharing with and without older siblings impacts condition, and the results support the hypothesis that young spiders can benefit by sharing prey captured by older siblings. Young spiders commonly shared prey with their older siblings, and in 6 of 20 trials, where young spiders were paired with an older sibling, the young spider gained more weight than the weight of the small prey item provided, indicating that it shared extensively on the large prey item captured by the older sibling. The condition of spiders with older siblings improved more than spiders feeding alone (Matched pairs test: $t = 3.9$, $p = 0.001$) and spiders feeding with siblings of the same age (Matched pairs test: $t = 5.3$, $p < 0.0001$). The condition of spiders feeding alone improved more than spiders feeding with siblings of the same age, but the difference was not significant (Matched pairs test: $t = 2.1$, $p = 0.053$).

Discussion

We tested the importance of prey sharing indirectly by examining how the condition of spiders varies with the presence of siblings of different ages both in the field and under laboratory conditions. In the field, we found that young spiders third to fifth instar were heavier in the presence of older siblings. Older spiders gained no similar benefit from older siblings, nor did any spider benefit or suffer from younger siblings. These results satisfy both predictions of the hypothesis that young spiders benefit from sharing prey with older siblings, suggesting that even though prey sharing is rare, it provides a significant benefit for individuals that are less capable hunters and require only a relatively small amount of prey for sustenance. Our laboratory data further show that sharing prey in a confined space, similar that of a bark retreat, can benefit small spiders because they gain access to large prey caught by older siblings.

We further tested alternative hypotheses that might explain the association between good condition in young spiders and the presence of older siblings. None of these hypotheses was supported by the data. If environments exceptionally rich in prey are responsible for the association between heavy spiders and multiple cohorts, all spiders should be heavier and colonies should be larger, as the adult female produces more egg sacs and fewer spiders die of starvation. Instead, improved condition was restricted entirely within the younger instars, and there was no association between colony size and condition. If either decreasing female fecundity or the preferential cannibalism of younger siblings with poor condition is responsible for the association between heavier spiders and the presence of older siblings, we would expect subsequent cohorts to be smaller than first cohorts. Instead, subsequent cohorts were the same size as first cohorts.

The data strongly support the conclusion that small spiders benefit from the presence of older siblings. The results of our laboratory experiment support prey sharing as the likely mechanism behind this benefit, as prey sharing in a confined space is common and large spiders do not monopolize prey. Third instars were heavier when their older siblings were larger, supporting the assertion that size asymmetries among siblings allow smaller spiders to benefit from prey sharing. However, mechanisms other than directly sharing prey are also possible. Young spiders, particularly third instars, readily scavenge for bits of masticated prey and dropped limbs at the bottom of the retreat (pers. obs.). The direct sharing of prey may therefore not be necessary for younger spiders to gain resources from older siblings.

Prey sharing is common to many social spiders and serves a variety of functions. Prey sharing allows for more efficient feeding, as each spider expends less digestive enzymes, and the combined enzymes break the prey down more quickly (Amire et al. 2000; Schneider & Bilde 2008; but see Ward & Enders 1985 for a decrease in feeding efficiency). Prey sharing is also a means by which the parental generation cares for the offspring (e.g. Marques et al. 1998; Evans 1998). While there are reports of larger (though not necessarily older) spiders sharing food with their smaller siblings (i.e. Marques et al. 1998), we provide the first evidence in spiders that, on average, older siblings improve the fitness of younger siblings. Whether *D. cancerides* is exceptional in this regard awaits further study on other species, but we note that many other social spiders produce a single clutch per female under field conditions, so that siblings sharing prey are roughly equal in size (Jacson & Joseph 1973; Schneider & Lubin 1997; Marques et al. 1998; Kim et al. 2005; Viera et al. 2007). *Delena cancerides* is unusual

in the tremendous size variation within a single generation (Fig. 1), and this heterogeneity allows small spiders to benefit by scrounging off of their older siblings to a degree that would be impossible in the single brood social spiders.

The benefits young spiders derive from their older siblings helps explain why spiders remain in groups even without an adult female. Yip and Rayor (2011) found that parental care provided the most important benefits for young spiders in the natal nest, and Yip et al. (in press) found that young spiders (third to sixth instar) moved into adjacent colonies rather than stay in their natal retreat after it had been abandoned by their mother. When young spiders do remain in their natal retreat without their mother, usually older siblings are present. All eight of the orphaned colonies collected in this study had at least one spider seventh instar or older along with younger siblings. From the older spiders' perspective, allozyme analyses have shown that most offspring in the colony are full or half siblings (Yip et al. 2012), so older spiders gain some amount of inclusive fitness from the presence of younger siblings while suffering relatively little cost. Thus, even though prey sharing may be infrequent and difficult to observe in the field, it may help maintain group cohesion, particularly in the absence of the adult female.

Our data suggest that older spiders and their younger siblings conform to an asymmetrical producer-scrounger model (Giraldeau and Beauchamp 1999), where the payoff for each tactic varies with age. Similar age-dependent tactics have been found in some birds, where younger group members that are inefficient foragers adopt the scrounger role (Verbeek 1977; Steele and Hockey 1995; Goss-Custard et al. 1998). Goss-Custard et al. (1998) found that, as the season progressed, juvenile oyster

catchers became better at foraging for mussels and their rate of scrounging declined. In this study, we did not track individuals over time. Interestingly, the age at which *D. cancerides* spiders no longer benefit from older siblings, demonstrated by our data here, coincides with the age at which spiders stop attempting to share prey with the mother (sixth instar and older; Yip & Rayor 2011). Presumably, if spiders could continue to benefit from sharing prey with older spiders they would, suggesting that this is the age at which a spider's resources are better spent as a producer.

It is not a general rule, however, that younger and less efficient feeders adopt the scrounger tactic. In some birds, older individuals scrounge from younger individuals (Burger & Gochfeld 1981), and, generally, dominant individuals are expected to maximize their fitness by exploiting the food produced by subordinates (Barta & Giraldeau 1998). Large *D. cancerides* spiders probably do steal food from younger spiders occasionally, and we have observed such behavior in the laboratory. However, two factors allow young spiders to be the predominant scroungers. One is, again, the dramatic size variation among siblings. It may simply be unprofitable for a 716 mg spider (the average weight of an eighth instar) to steal the small prey of a 17 mg spider (the average weight of a third instar), while the reverse is not true. The second factor may be that spiders, regardless of size or dominance, are poorly equipped to defend their kill. The chelicerae, and their associated venom glands, are a spider's primary weapons, and when they are engaged in feeding, a spider is largely helpless and must run from an aggressor or drop the prey. In a confined space, such as a bark retreat, spiders may be forced to share with siblings, and there is some evidence to suggest this to be true. In field colonies, older spiders (primarily the adult female) shared when more

juveniles were present, and juveniles appeared to overwhelm the capturing spiders' efforts to secure the prey (Yip & Rayor 2011).

We have thus far interpreted the relationship between young spiders and their older siblings as a producer-scrounger game. Because younger siblings obtain prey through their older siblings, this could be considered an example of incipient alloparental care, although we lack evidence that older siblings are actively feeding younger individuals, as in the cooperative breeding birds (Koenig et al. 1992; Hatchwell 2009). Prey sharing in *D. cancerides* is similar to 'tolerated theft' described in primate literature, in which one individual allows another to take a share of food (Blurton Jones 1984). It has been noted that there is little functional difference between tolerated theft and cooperation (Blurton Jones 1984), demonstrating that the line between exploitation and cooperation can be fine. In other social spiders, it is often the case that more spiders feed on a prey item than attempted to capture it (e.g. Ward 1986; Kim et al. 2005), and so some spiders benefit from the cooperation of others while avoiding its costs. In this case, the difference between cooperation and exploitation may change depending on when spiders arrive at the site of prey capture: early arrivals aid the attack and late arrivals feed on the spoils (Kim et al. 2005). 'Cheating' such as this is thought to threaten the stability of cooperative societies; however, the destabilizing effects of cheating are mitigated if the participants are related (Sachs et al. 2004). In *D. cancerides*, relatives may compete over individual prey items, but, on average, interactions over prey act as cooperation for young spiders that benefit from older siblings. In addition, we did not detect a cost of competition for older siblings, suggesting that if there is a cost to sharing prey with younger siblings, it is relatively

small. Therefore, the producer-scrounger system, that might be exploitative in one context, can be cooperative and a benefit to group living in a context where the benefits of feeding a relative outweigh the costs.

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Table 1

Instar	Effect	Test Statistic	Effect on Condition	n	p-value
3rd	Older Siblings	$F_{1,137.3} = 20$	+ 0.089	711	<0.0001**
	Younger Siblings	NA	NA		NA
	Season	$F_{1,30.6} = 22$	- 0.053		<0.0001**
	Adult Female	$F_{1,41} = 5.3$	+ 0.13		0.026*
4th	Older Siblings	$F_{1,93.5} = 5.3$	+ 0.055	437	0.024*
	Younger Siblings	NA	NA		NA
	Season	$F_{1,45.9} = 9.5$	- 0.035		0.0034**
	Adult Female	$F_{1,58.8} = 2.3$	- 0.08		0.13
5th	Older Siblings	$F_{1,468.2} = 7.3$	+ 0.033	546	0.007**
	Younger Siblings	$F_{1,314.2} = 0.56$	- 0.016		0.45
	Season	$F_{1,53.1} = 11.1$	- 0.034		0.002**
	Adult Female	$F_{1,80.5} = 3.2$	- 0.072		0.080
6th	Older Siblings	$F_{1,71.1} = 2.1$	+ 0.034	460	0.15
	Younger Siblings	$F_{1,399.5} = 0.63$	+ 0.0098		0.43
	Season	$F_{1,49.9} = 7.0$	- 0.031		0.011*
	Adult Female	$F_{1,60} = 0.48$	- 0.027		0.49
Subadult	Older Siblings	$F_{1,436.2} = 0.003$	+ 0.0021	443	0.95
	Younger Siblings	$F_{1,221.5} = 0.05$	- 0.0039		0.82
	Season	$F_{1,35.1} = 3.9$	- 0.024		0.056
	Adult Female	$F_{1,52} = 0.026$	+ 0.005		0.87

Table 1. Summary statistics for the correlations between condition and the presence of siblings, the presence of the mother, and season applied to each instar and subadults. Third and fourth instars were too young to have younger siblings, so this effect is N/A for these instars. * p-value < 0.5 ** p-value < 0.01

Table 2

	Instar	Effect	Test Statistic	Effect on Condition	n	p-value
Older Siblings	3rd	# Older Siblings Average size difference	$F_{1,8.5} = 1.9$ $F_{1, 9.6} = 7.8$	+ 0.007 + 0.084	433	0.20 0.02*
	4th	# Older Siblings Average size difference	$F_{1,30.9} = 0.43$ $F_{1, 36.8} = 0.11$	+ 0.002 - 0.009	188	0.52 0.75
	5th	# Older Siblings Average size difference	$F_{1,110} = 1.8$ $F_{1, 49.9} = 0.19$	- 0.003 + 0.009	214	0.18 0.67
	6th	# Older Siblings Average size difference	$F_{1,14.5} = 0.51$ $F_{1, 15.7} = 0.19$	- 0.006 -0.020	91	0.49 0.67
	Subadult	# Older Siblings Average size difference	$F_{1,2.2} = 1.1$ $F_{1, 3.8} = 0.84$	+ 0.24 + 0.13	9	0.40 0.41
Younger Siblings	5th	# Younger Siblings Average size difference	$F_{1,18} = 1.7$ $F_{1,18.4} = 0.75$	- 0.004 - 0.23	46	0.20 0.40
	6th	# Younger Siblings Average size difference	$F_{1,96} = 2.24$ $F_{1,180.8} = 0.25$	+ 0.004 + 0.033	197	0.14 0.62
	Subadult	# Younger Siblings Average size difference	$F_{1,40.4} = 1.1$ $F_{1,140.4} = 1.1$	+ 0.002 - 0.017	342	0.30 0.30

Table 2. Summary statistics for the correlations between condition and the number of siblings and the average size difference between a given spider and its siblings. Older and younger siblings are considered separately. The effects are controlled for the presence of the mother and season but their statistics are omitted here because their effects on condition are given in Table 1 with a more complete data set. * p-value < 0.5

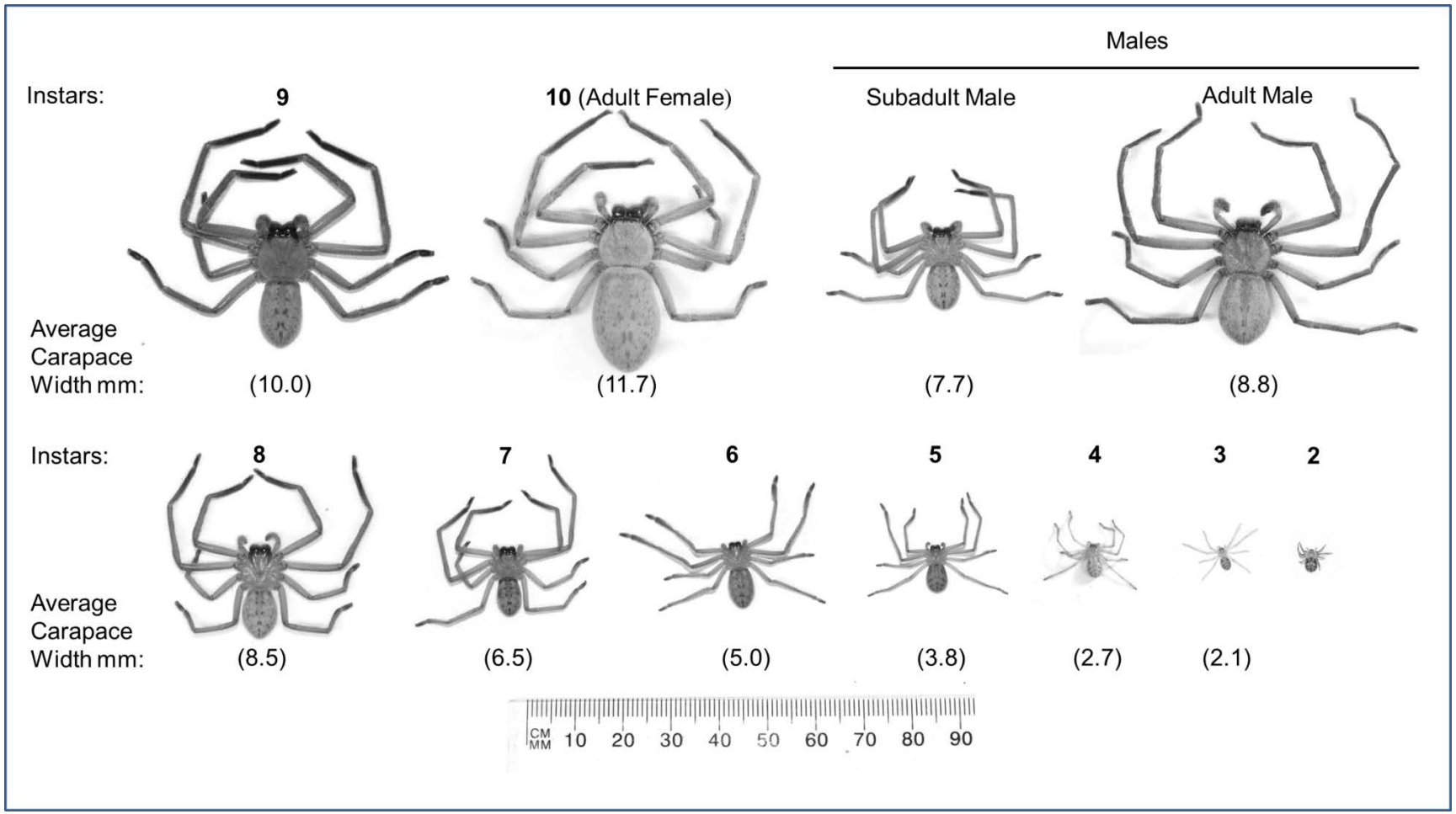

Figure 1. The size of *D. cancerides* instars. Mean carapace width was calculated from 984 spiders collected from Canberra, Australia. They were assigned instars based on size differences among individuals and on our experience with laboratory animals. Note that all instars are concurrently represented in some colonies.

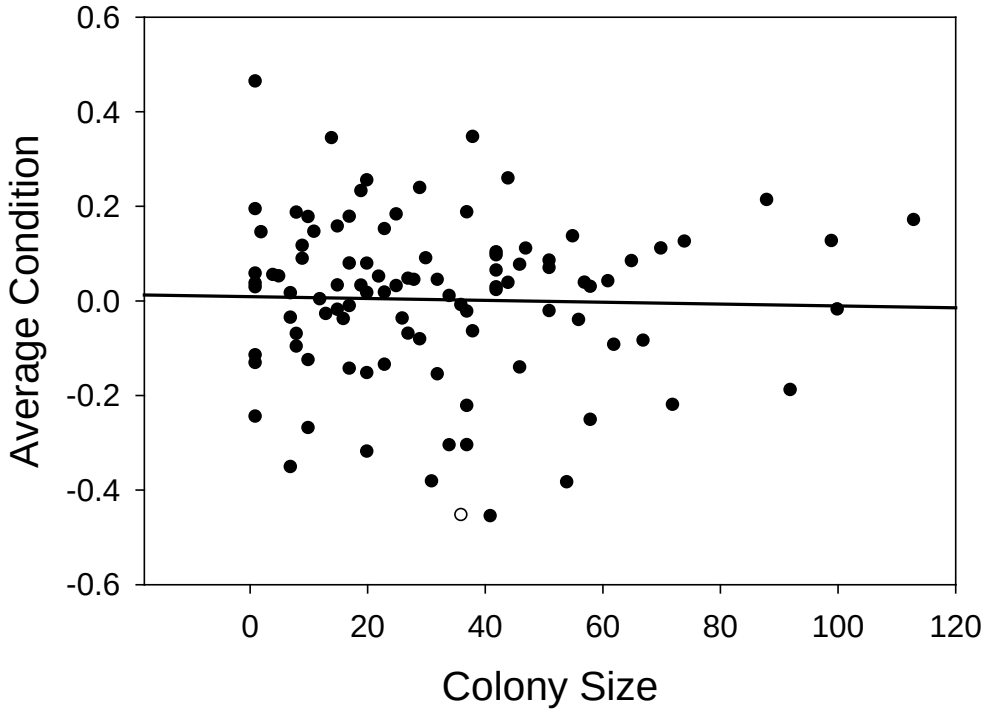

Figure 2. The average condition of colonies (including single adult females) in relation to the number of individuals in the colony. The solid line represents the regression line between average condition and colony size.

Supporting information

The effect of prey capture on condition

Methods

We performed a laboratory experiment to determine if prey capture correlates with condition as we define it. To test the effect of prey capture on condition, 46 spiders were housed individually in 17x11x4 cm plastic tubs. Twenty-three were fed 2/week (high prey), and 23 were fed 1/week (low prey). We weighed the total prey given to each spider to the nearest 1/10 mg. and removed prey items that were dead but not eaten at the next feeding. Because prey may have desiccated in that time, we subtracted the average weight of prey items from the previous feeding when prey remained uneaten. We measured spiders' weight, carapace width, and second leg length prior to commencement of the feeding regimen, three weeks into the regimen, and at termination of the regimen after five weeks. Condition was calculated as we did under 'Condition of spiders in the field,' except that only carapace width and molting status were included as predictors of weight, as other variables did not explain a significant portion of weight variance. Six spiders, three in each feeding regimen, died prior to measuring at three weeks, and two spiders under the low food regimen and one spider under the high died between measuring at weeks three and five. We analyzed the relationship between feeding success and change in condition using a combination of ANOVA, Welch ANOVA, and Wilcoxon (rank sums) tests, depending on whether the data in high and low treatments had equal variances and whether the residuals were normally distributed. We also examined the relationship between feeding success and

condition as a linear regression between total food consumed and change in condition. Statistics were run in JMP.

Results

The amount of food spiders ate positively correlated with condition (Fig. S1). During the first three weeks of the feeding regimen, the change in the spiders' condition was significantly greater for those under the high feeding regimen than the low (high mean change in condition = 0.29; low mean change in condition = -0.09; Wilcoxon Rank Sum Test $\chi 2 = 12.94$, $n = 40$, $p = 0.0003$). Condition also increased with the amount of food eaten during this period ($R^2 = 0.16$, $n = 40$, $t = 2.72$, $p < 0.0099$). Between week three and week five, the change in condition did not differ between high and low regimen spiders, and this was mainly because the condition of high food spiders ceased to improve (high mean change in condition = -0.08; low mean change in condition = -0.04; Welch ANOVA $F_{1,35} = 0.07$, $p = 0.79$). Correspondingly, the correlation between amount of food eaten and change in condition is not significant between three and five weeks ($R^2 = 0.08$, $n = 37$, $t = 1.75$, $p = 0.09$). The total change in condition over the five week period remained significantly higher for high regimen spiders than low (high mean change in condition = 0.21; low mean change in condition = -0.12; ANOVA: $F_{1,35} = 9.78$, $p = 0.0035$). The total food eaten over the five week period positively correlated with change in condition ($R^2 = 0.24$, $n = 37$, $t = 3.30$, $p = 0.002$; Fig. S1).

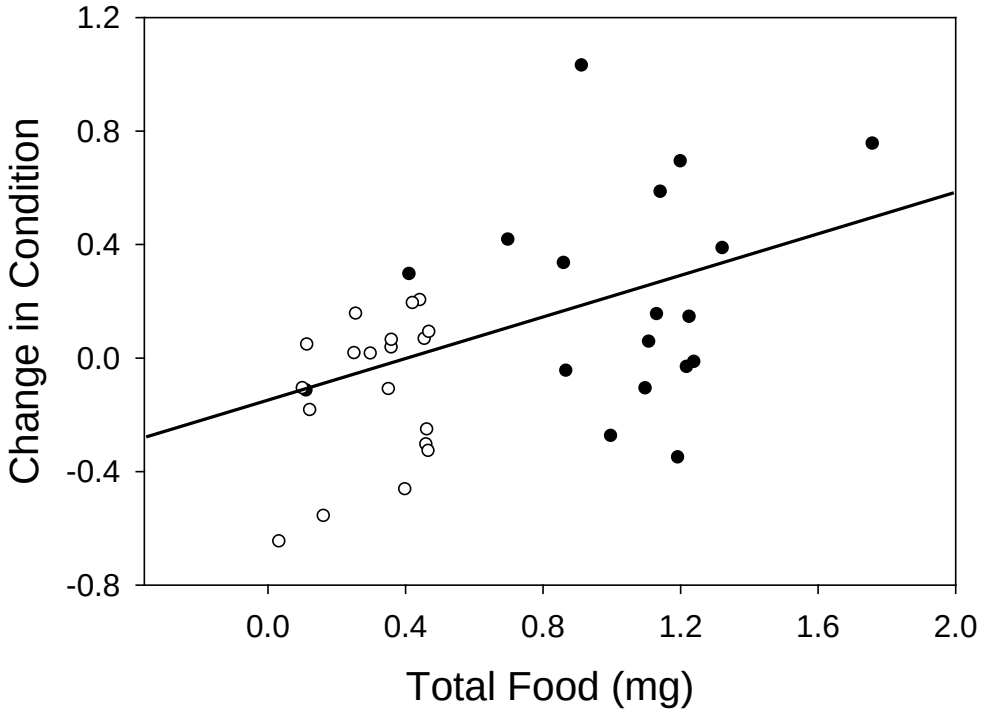

Figure S1. The effect of total prey consumed on change in condition, where ○ indicate spiders on the low prey feeding regimen, and ● indicate spiders on the high prey. The line is the simple regression between total prey consumed and change in condition over the entire 5 week period.

CHAPTER 5

Saturated habitats promote philopatry in a social huntsman spider

E.C. Yip, L.S. Rayor

Abstract. The saturation of suitable habitats is known to promote philopatry in a variety of animals; however, the role of habitat saturation has been tested as a proximate cause leading to a change in dispersal behavior, rather than as a possible ultimate cause for philopatry. The social huntsman spider, *Delena cancerides* (Sparassidae), lives exclusively under the bark of certain trees, and suitable retreats are rare. To test the hypothesis that habitat saturation is an ultimate cause of delayed dispersal from the natal retreat, we experimentally released marked adult females at 30 sites with artificial retreats or 'nest boxes' to determine how retreat availability affected potential competition over the retreats. Dispersal for small spiders was costly. Sites with fewer available retreats had greater nest box occupancy, larger nest box occupants, and more frequent usurpation of nest boxes by larger spiders. Occupancy was high at most sites. Spiders therefore benefit by staying in the natal bark retreat until they are larger and the most competitive for a rare retreat.

Key words: Aggression, Dispersal, Ecological constraints, Habitat saturation, Philopatry, Social, Spiders

Main text

The ecological constraints hypothesis posits that philopatry results when animals postpone or forgo dispersal from their natal site because of strong ecological constraints on solitary living (Emlen 1982). A principal source of ecological constraint is a habitat in which suitable territories or breeding sites are saturated, leaving few options for dispersing individuals, i.e. the 'habitat saturation hypothesis' (Selander 1964; Koenig et al. 1992). With few options available, dispersing individuals must spend more time and energy searching for habitat, thereby raising the costs of dispersal relative to philopatry. The common need for habitat and shelter makes habitat saturation appealing as a general agent promoting philopatry and group formation, and habitat saturation has been credited for the delayed dispersal in a wide variety of taxa, including mammals (Blumstein & Armitage 1999; Schradin et al. 2010), birds (Komdeur 1992), fish (Wong 2009), and hymenopterans (Pedersen & Boomsma 1999).

However, these studies have examined how dispersal decisions change with the degree of habitat saturation, either through the manipulation of habitat availability (Hebers 1986; Pruett-Jones & Luis 1990; Komdeur 1992; Walters et al. 1992) or through correlations between dispersal and population density (Koenig et al. 1992; Hatchwell 2000; Hayes 2000), and thus test habitat saturation as a proximate mechanism promoting delayed dispersal (Komdeur & Ekman 2010). Habitat saturation, may also act as an ultimate cause by increasing the costs of dispersal and selecting for low fixed probabilities of dispersal over evolutionary time. Tests of the habitat saturation hypothesis that rely on changes in animal behavior presuppose that individuals are plastic in their dispersal behavior and can assess current habitat abundance prior to

risking dispersal. This may not always be true. In some polygynous ants, philopatric queens are morphologically distinct from dispersing queens of the same species (Bourke & Heinze 1994), indicating that individuals lose dispersal plasticity during development. Some philopatric queens may never leave their natal colony (Dalecky et al. 2005), indicating that they have limited information about current habitat availability. To test the habitat saturation hypothesis as an ultimate cause of delayed dispersal, without invoking any particular proximate mechanism for dispersal, we document that habitat saturation makes early dispersal costly. We measured the degree of habitat saturation at 30 field sites, correlated the intensity of competition for habitat with habitat saturation, and showed that philopatry helps individuals secure a habitat in the future.

We use this approach in the Australian huntsman spider, *Delena cancerides*, an unusual social spider that lacks both a capture web and a silken retreat. Instead, these spiders live under the exfoliating bark of dead trees in large family groups, consisting of one mother and one or more cohorts of young (Rowell & Avilés 1995; Avilés 1997). The offspring, which can number up to 200, remain in the natal nest until sexual maturity, at about 1 year and well beyond the age of independence (Rowell & Avilés 1995; Rayor et al. in prep.). Their reliance on a bark retreat constrains their dispersal options and makes these spiders particularly well-suited to examine habitat saturation. Delineating what constitutes a 'suitable habitat' is notoriously difficult (Keller 1995), but the pieces of bark conforming to the criteria preferred by spiders (see Supporting information) are discrete and quantifiable. The occupancy of bark retreats is over 90% at 53% of collection sites and averages 80% across all collection sites (Rayor et al. in prep.). Laboratory data show that larger spiders almost always push smaller individuals out of

artificial nest boxes when only one box is provided (see Supporting information), and field data show that subadults usually cannot co-occupy a retreat with an unrelated adult female (Yip et al. 2012). Thus, one reason why subadults remain in the natal retreat may be to postpone retreat competition until they are larger and more competitive. Rowell and Avilés (1995) first hypothesized that the social behavior of *D. cancerides* was the result of habitat saturation of bark retreats, but this has not been tested until now.

We tested the habitat saturation hypothesis by comparing retreat competition among field sites with varying retreat abundance. To make comparisons among sites, we needed to quantify both the number of competitors and the availability of resources. Alternative retreat sites under bark varied naturally and could be quantified at each site; however, it was impossible to quantify the number of naturally occurring *D. cancerides* spiders without destroying their bark retreats and disrupting their colonies. Instead, to compare competition from site to site, we standardized the number of competitors by releasing 15 marked virgin adult females (the age at which spiders would be seeking new retreats) at each site. We supplemented each site with artificial nest boxes (Fig. 1), which could be opened without disrupting the colony to allow us to record maximum percent occupancy of nest boxes, average occupant size, and rate of nest box usurpation. We then examined the correlation between these measures and the number of available retreats within 50 m. We hypothesized that, if habitat saturation promotes philopatry through increased retreat competition, (1) nest box occupancy should be high. (2) Competition should intensify with fewer available retreats, leading to increased nest box usurpation. (3) Spiders usurping the nest boxes should be larger

than previous residents, leading to (4) larger occupants when retreats are fewer. The confirmation of these predictions would demonstrate that dispersal is more costly for smaller spiders and that individuals should delay dispersal until they are adults and maximal size for effective competition for retreat sites.

Maximum occupancy by marked adult females averaged 75% ± 24% S.D. across all sites (Fig 2A). If all *D. cancerides* occupants are included (both marked and unmarked, naturally occurring spiders in the area), maximum occupancy averaged 89% ± 14% S.D, with 18 of 30 sites (60%) at full occupancy (Fig 2B). Maximum occupancy by both marked adult females and all spiders decreased with retreat availability (marked females only: Spearman's $\rho = -0.68$, $p < 0.0001$; all spiders: Spearman's $\rho = -0.58$, $p = 0.0007$). The average size of the marked adult females that moved into nest boxes increased with fewer empty retreats (Fig 3A; Spearman's $\rho = -0.53$, $p = 0.0029$). Sites with fewer empty retreats had more spiders replaced by other spiders per observation (Fig 3B; Spearman's $\rho = -0.37$, $p = 0.046$), and spiders that usurped retreats were usually larger than the original resident, both when the usurpers were only marked adult females and for all (both marked and unmarked) usurpers (marked females only: mean difference between coxa-coxa width = 0.83 mm; $t = 2.5$, $n = 24$, $p = 0.02$; all spiders: mean difference between coxa-coxa width = 1.6 mm; $t = 6.0$, $n = 45$, $p < 0.0001$).

In addition to nest box turnover, there was direct evidence for aggression related to retreat competition. Seven adult females were found dead at the base of nest boxes. An additional two nest boxes had *D. cancerides* legs at the bottom. Dead spiders or legs were more likely to be found in areas with fewer retreats, but the association was not significant (Fig 3C; Spearman's $\rho = -0.29$, $p = 0.12$).

As predicted, habitat saturation was widespread, with the occupancy of nest boxes reaching 100% at a majority of sites, and larger spiders increasingly eliminated smaller spiders from nest boxes as retreat abundance declined. These results provide strong evidence for intense retreat competition and that younger (and therefore smaller) spiders are at a competitive disadvantage for securing a retreat. Younger spiders should therefore stay in the natal retreat until they are as large as possible before dispersing and competing for a new retreat.

The high degree of habitat saturation for *D. cancerides* could be due to recent anthropogenic changes or due to sampling bias, where only very dense populations were sampled (Koenig et al. 1992). If this were the case, we would not expect habitat saturation to have selected for delayed dispersal across the species. However, we believe our sites represent historically typical environments for these spiders. Some of our collection sites were along roads or sheep paddocks, where trees had been removed and dispersal options were very limited. However, most of our sites (24/30) were located in unaltered bushland where trees were unmanaged and bushfires were allowed to occur. Most eucalypts (*Eucalyptus* and its related genera), which dominate the flora, do not provide suitable bark retreats (Rayor et al. in prep.), leaving even natural sites with more than a handful of available retreats very rare. Only three of our sites had more than six available natural bark retreats within a 50 m radius simply because we could not locate any other retreat-rich environments within 60 km of Canberra, Australia. This paucity of suitable retreats has likely persisted through evolutionary time, as eucalypt species began proliferating throughout Australia 60 Ma

(Crisp et al. 2004), and eucalypt pollen dominated the Canberra region by the late Pliocene (Truswell 1993).

The decision to disperse or to remain philopatric depends on the sum costs and benefits of these two alternatives. Habitat saturation and the cost of competing for a rare retreat are a critical component of this calculus but must be considered alongside the costs and benefits of staying in the natal retreat to understand dispersal timing. If dispersal costs alone were driving dispersal timing, we would expect females to wait until the final molt when they are the most competitive for a retreat, yet we often collected single penultimate females with or without adult male consorts (Rayor et al. in prep.). Previous study on the benefits of group living in this species found that spiders lose foraging and defense benefits within their natal colony as they mature (Yip & Rayor 2011). In addition to declining benefits, spiders may face increasing costs in the form of aggression by sisters attempting to inherit the natal retreat. Only one female breeds per colony, and other than newly mature daughters, no other adult females are tolerated in the colony (Rayor et al. in prep.). Retreats, if they remain securely attached to the trunk, may be continuously inhabited for several generations, and laboratory data show that these spiders become increasingly aggressive to each other as they approach maturity (Yip et al. 2009). Behavioral data in field colonies as daughters begin to mature are difficult to collect, but aggressive interactions among these penultimate and newly adult daughters are likely to increase the cost of staying in the retreat. Prior to conflict among maturing sisters, however, there is little cost to remaining in the natal retreat, as prey competition within the retreat is low (Yip & Rayor 2011). Therefore, any

substantial cost to dispersal should promote philopatry until either maturity or eviction by an older sister.

Support for the habitat saturation hypothesis in a spider suggests that this hypothesis is broadly applicable beyond the social vertebrates and eusocial insects. We also show how habitat saturation can promote philopatry as an ultimate cause without relying on particular proximate causes, such as the ability of individuals to assess current, local habitat availability to determine their dispersal timing. It is currently unknown whether individual *D. cancerides* spiders are capable of assessing retreat availability and adjusting their behavior. Spiders generally have poor mobility and eyesight compared to birds, mammals, fish and hymenopterans (Foelix 2011), making them comparatively inefficient at sampling the habitat to obtain information. Even if spiders can modify their dispersal behavior, incomplete information that is costly to obtain and the usually high variance of ecological field data might make the influence of habitat saturation on individual dispersal behavior undetectable. Our methods circumvent this problem and suggest that habitat saturation as an ultimate cause for delayed dispersal might be applicable to other social organisms with limited mobility, such as social lizards (Chapple & Keogh 2005; Davis et al. 2011) or in organisms for which habitat manipulations have failed to elicit changes in dispersal behavior (Bull & Schwartz 1996).

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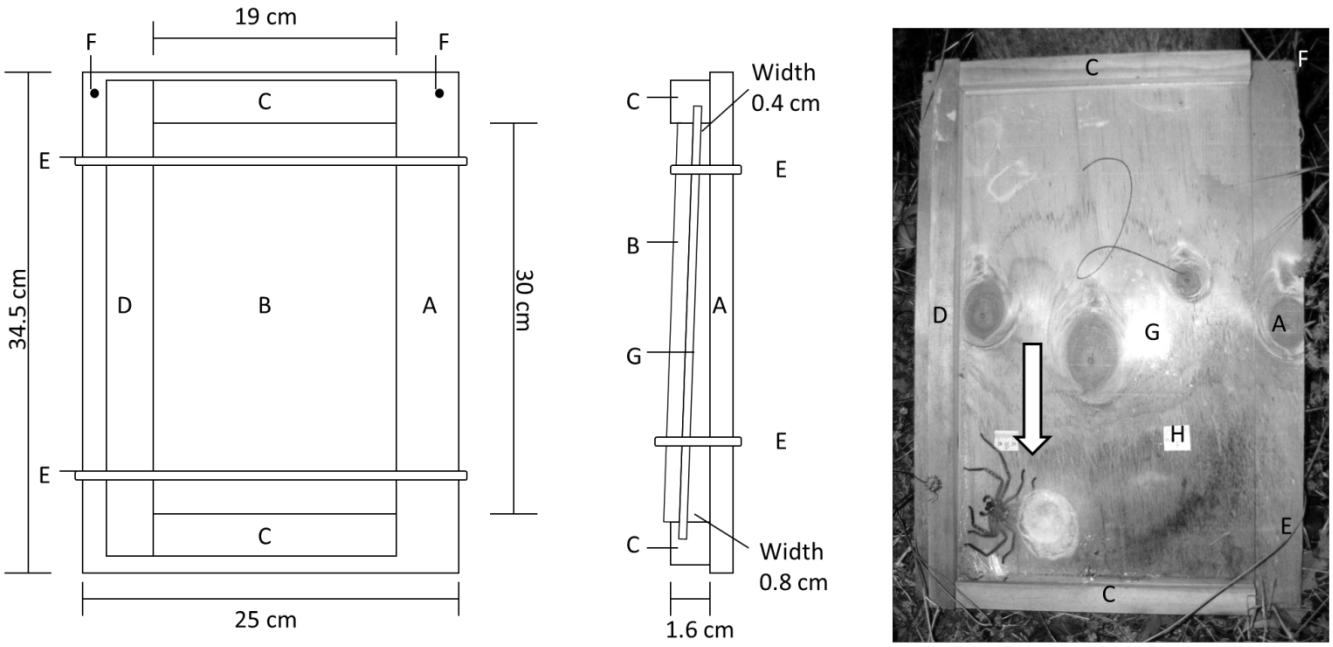

Figure 1.. Nest box design: (A) Plywood back; (B) Plywood cover; (C) 1.6 cm square dowel base and top and with 4 mm groove; (D) Side; (E) Wire to secure cover; (F) Holes to secure box to the base of a tree; (G) plastic sheet inserted into groove; (H) Small ruler used as a reference to measure spider sizes from photographs; Interior dimensions: 19X30X0.8-0.4. The arrow indicates an adult female and her egg sac with developing spiderlings. The specifications of the nest box were determined by choice tests in the laboratory (see Supporting information).

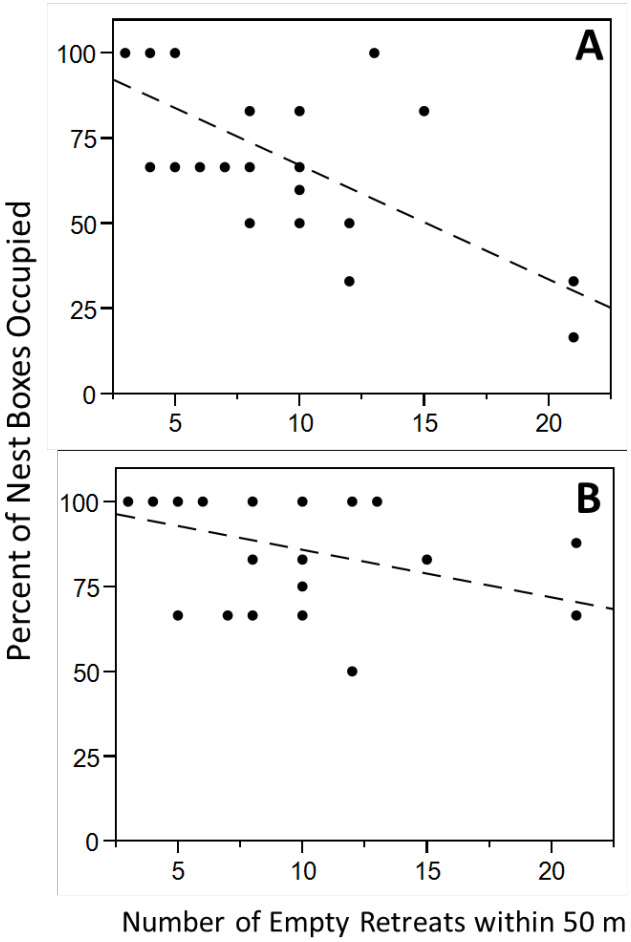

Figure 2. The highest percent occupancy of nest boxes recorded in a single night plotted against the number available retreats within 50 m of each site. The number of available retreats is the sum of natural bark retreats and nest boxes. The number of bark retreats, without nest boxes, varied from 0-15. Only marked adult females are included in (A) and both marked and unmarked *D. cancerides* spiders are included in (B). Dashed lines represent the linear regression line.

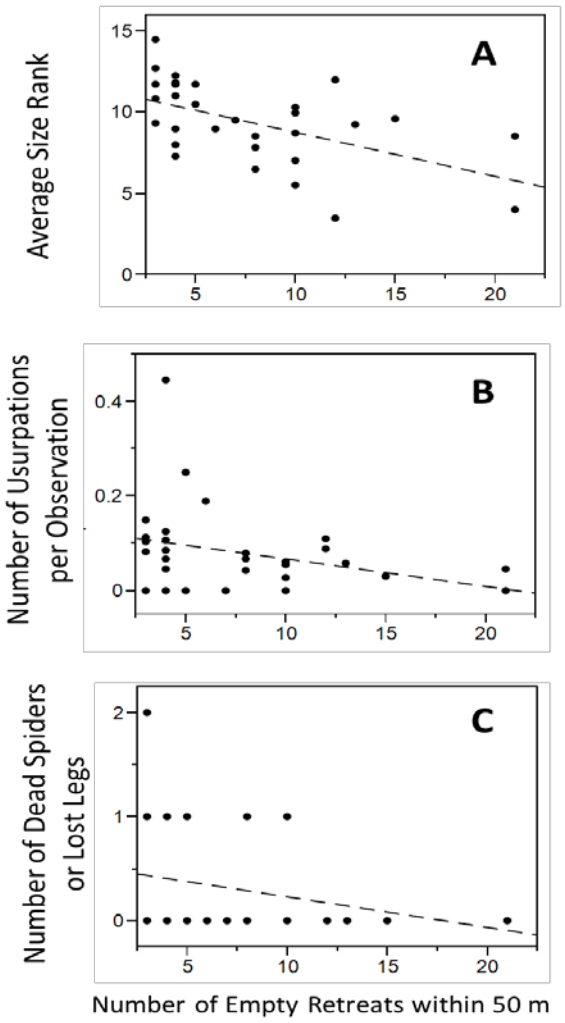

Figure 3. Three measures indicative of retreat competition plotted against the number of available retreats within 50 m of each site. (A) shows the average size of marked adult females occupying the retreats. Size was measured as their size rank relative to all 15 marked females released at each site, with 1 being the smallest and 15 the largest; (B) shows the number of usurpations per observation, and (C) shows the number of dead spiders or lost legs found in or just outside nest boxes. Dashed lines represent the linear regression line.

Supporting information

Materials and Methods

Nest Box Preference

Retreat Competition in the Laboratory

Materials and methods

We selected 30 sites within 60 km of Canberra, Australia and collected 72 colonies (a family group living under a single piece of bark), totaling 2063 spiders, from these sites from August to December 2009. Sites were separated by at least 250 m. These spiders were reared in the laboratory until adulthood. Most spiders were kept separately in plastic tubs (17x12x3.8 cm, with at least 20 ventilation holes) so we could to care for spiders individually and thus minimize mortality and chance of escape. It was impractical to house and feed spiders younger than fifth instar individually, so these spiders were kept together with the adult female and separated out as they became larger subadults. Small groups were housed in plastic tubs, but larger groups (10+) were housed in glass terraria. In the wild, spiders remain in the retreat during the day and only leave the retreat at night, so they are never exposed to direct sunlight. To protect spiders in the laboratory from direct exposure to light, we added two pieces of plywood (15cm x 25 cm) held 0.7 cm apart by Velcro to glass terraria as a retreat. Plastic tubs were kept in cardboard boxes to shield spiders from direct light. Light was maintained at a 12-12 light-dark cycle, with ‘dawn’ and ‘dusk’ simulated by 4 incremental changes in light intensity over 1 h. Spiders were fed once per week on commercially purchased house crickets (*Acheta domesticus*). Spiders were given a

spray of water if they were approaching a molt or if their abdomens appeared shriveled. Seventy-two spiders died before their release, for a mortality rate of 3.5%.

We placed three nest boxes (Fig. 1) at 16 sites with few dead trees. Fourteen sites with an abundance of dead trees were given 6 nest boxes to increase the chances of observing the spiders in the nest boxes when there were other retreat options available in the environment. We affixed nest boxes with steel wire to the base of trees. We thoroughly examined each site for available natural retreats within 50 m of any nest box. A piece of bark was available if it met three criteria: (1) area under the bark > 200 cm^2; (2) distance between the trunk and bark 5-10 mm; (3) firm attachment of the bark to the trunk (i.e. the bark could not be shifted by hand more than 1-2 cm in any direction). These criteria were based on retreat characteristics from collection data (Rayor et al. in prep.) and laboratory choice tests (see Nest Box Preference). We searched for available retreats up to 2.5 m high. It is possible that more available retreats were above this height. However, as tree trunks taper with height, pieces of loose bark large enough to be suitable retreats become increasingly rare, and we have only once found suitable retreats when searching above 2 m (Rayor et al. in prep.). We believe we did not miss many available retreats. The total retreat abundance for each site was the number of natural retreats plus the number of nest boxes.

Prior to release, we measured the carapace width and the distance between the coxa of the second legs for each adult female as a measure of body size from both the dorsal and ventral view. Each adult female was given a unique number using permanent marker on the carapace, and a unique pattern of dots and slashes on the sternum. We refer to the spiders we released as ‘marked spiders,’ while ‘unmarked’

spiders refer to other, naturally occurring *Delena cancerides* spiders in the area that moved into nest boxes. At each site, 15 marked virgin females were released at dusk in a random order. Fifteen females correspond to the dispersal of about two colony's offspring (Rayor et al. in prep.). As multiple colonies are often within 50 m of each other (Rayor et al. in prep.), this is a realistic number of spider competitors. They were coaxed out of their plastic tubs onto different trees haphazardly selected in the area. We released the first group of adult females 1 February 2010. We released spiders at another 8 sites during the austral autumn, with the last group released 29 April 2010. The weather became cool in May, with an average daily low of 3.1 C for the month (Australian Government). Spiders only rarely leave the retreat at low temperatures, so no more spiders were released until the spring. An additional 21 groups of spiders were released starting 6 October 2010 (average low for the month = 7.2 C, (Australian Government) and ending 7 December 2010. Season (spring or fall) did not affect occupancy of nest boxes (Wilcoxon rank sums: $\chi 2 = 1.6$, df = 1, $p = 0.2$), occupant size (Wilcoxon rank sums: $\chi 2 = 1.2$, df = 1, $p = 0.28$), or the rate at which nest boxes were usurped (Wilcoxon rank sums: $\chi 2 = 0.05$, df = 1, $p = 0.82$), so data from both seasons are pooled.

After releasing spiders, we examined the nest boxes at each site for the next three nights and once a week thereafter. We observed all sites for 5 weeks to record occupancy, identity and size of marked females, size of any unmarked occupants, and resident turnover. We photographed the nest boxes to record the size of unmarked spiders. Rulers taped to the inside of each nest box (Fig. 1) allowed us to estimate spider size from the photographs. To prevent light exposure from disturbing the

spiders, observations of nest boxes began at dusk and continued until as late as 01:00 am. In addition, we continued observations at sites with spiders released earlier in the season for up to 2 months to record additional resident turnover.

Maximum occupancy was expressed as the highest percentage of nest boxes occupied during a single night. This is calculated for both marked adult females only and for all spiders (marked and unmarked), including adult males. Marked females released at each site were ranked in size, from 1, the smallest, to 15, the largest. We used the average size rank of marked nest box occupants to compare occupant size among sites. We estimated the size of unmarked spiders that occupied the nest boxes based on photographs. These unmarked spiders were not used to calculate average occupant size, but they were used to determine the size of usurping spiders relative to the previous occupant. We considered resident turnover to be 'usurpation' when a resident spider was replaced by a different spider in the subsequent observation. Transitions from an adult female to an adult male were not considered usurpation, as it is unlikely that adult males exclude adult females, and we have observed adult males and females cohabit for weeks. Because of variation in number of nest boxes and in total number of observations, the number of usurpations was divided by the number of observations per site. Maximum percent occupancy, average size of released spiders in nest boxes, and number of usurpations per observation were each compared to the number of available retreats within 50 m. No transformation made the regression residuals normally distributed, so we used the non-parametric Spearman's ρ to test for correlations. For each usurpation, we calculated the difference in coxa-coxa distance

between the usurper and the original resident and used a t-test to test if the average was significantly different from zero.

Nest box preference

To design a nest box attractive to the spiders, we conducted a series of choice tests to determine which nest box features adult female spiders preferred. We raised spiders descended from wild-caught specimens to adulthood in the laboratory. We selected forty adult females for three choice experiments that gave spiders a choice between retreats that differed in (1) area, (2) depth (the shallowest dimension of the box), or (3) size of the entrance to the retreat. Some spiders were used more than once total, but only once for each of the three different experiments. All spiders were mated prior to the experiment, by placing males with the females in 17x12x3.8 cm plastic tubs and video recording the tub to confirm mating. We placed spiders in glass terraria (25x42x51 cm) with several nest boxes assigned a random placement inside. These terraria were under a 12-12 light-dark cycle. Once per day, at roughly 24 h intervals, we examined the nest boxes to determine which nest box was occupied. We defined when the spider had made a 'choice' when she was in the same nest box for three consecutive observations. The trial ended either after the spider made a choice or after 10 days. Spiders that made no choice in that time were removed from analyses. We supplied crickets at the start of the experiment and sprayed the interior of the terraria with water one to two times during the trial.

Experiment 1: area

Thirteen spiders were separately placed inside terrariums, each with two nest boxes at opposite ends. One nest box was 27x20 cm (540 cm^2) in area, and the other was 21x11 cm (231 cm^2) in area. These sizes reflect a larger than average retreat and a small retreat based on collection data (Rayor et al. in prep.). Both nest boxes were 1 cm deep, and openings to both nest boxes were 10 cm.

Experiment 2: depth

Twenty-three spiders were separately placed inside terrariums, each with three nest boxes placed at either end and in the middle of the terrarium. All nest boxes were 27x20 cm (540 cm^2) with an opening of 27 cm. The depths of the nest boxes were 7, 10 and 12 mm.

Experiment 3: entrance size

Fourteen spiders were separately placed inside terrariums, each with three nest boxes placed at either end and in the middle of the terrarium. The nest boxes were 27x20 cm (540 cm^2) in area and 10 mm deep. The entrances to the nest box were 10, 22, or 27 cm.

Results

Ten spiders moved into the larger nest box, while only 1 moved into the smaller (Likelihood ratio $\chi 2$ test: $\chi 2 = 8.5$, $p = 0.0035$). Two spiders made no choice. Ten spiders moved into nest boxes with a 7 mm depth, 10 into nest boxes with a 10 mm depth, and three into nest boxes with a 12 mm depth. If the 7 and 10 mm deep nest boxes are considered together, they are preferred over 12 mm deep nest boxes (Likelihood ratio $\chi 2$ test: $\chi 2 = 5.0$, $p = 0.026$). Spiders preferred the wide opening of 27 cm, with 9 spiders choosing those nest boxes and only three choosing either the

medium (one spider) smaller (two spiders) opening (Likelihood ratio $\chi 2$ test: $\chi 2 = 8.7$, $p = 0.0031$). Two made no choice.

Retreat competition in the laboratory

We tested the role of spider body size on retreat competition in the laboratory. We selected three immature sisters from 12 families and raised them to adulthood (the three experimental sisters were raised together, but separate from the rest of the colony). Due to mortality, only seven family groups had all three sisters reach maturity. In the remaining five groups, two females per group reached maturity. We separated spiders as they matured, recorded their carapace widths, and placed them with adult males for mating (see mating methods under Nest Box Preference). After mating, each group of sisters was placed in a single terrarium (25x42x51 cm), with a single nest box (27x20 cm or 540 cm^2 in area; 10mm deep; 27 cm opening). We recorded occupancy of the nest box once per day, as in our nest box preference methods. A spider that was in the nest box for three consecutive days considered to have 'won' the nest box, terminating the trial. We then calculated the difference between the carapace width of the winning spider and the average carapace width of the sister group. We compared the average difference to zero to test the hypothesis that larger spiders won the nest box.

Results

Winning spiders were usually larger than their sisters (t test: $t = 3.9$, $p = 0.002$). The winning spider was larger than the average size in all but two cases, and in these two cases the difference was less than 0.3 mm.

CHAPTER 6

Maternal care and subsocial behavior in spiders

E.C. Yip, L.S. Rayor

Introduction

Virtually all spiders are predators; most are generalists that will feed on anything they can capture, and most spiders can capture prey larger than themselves. Cannibalism, of both mates and relatives, is common. It is perhaps unsurprising then that social behavior of any kind is rare in the spiders, with fewer than 80 out of 42,000 described species considered group living (Lubin & Bilde 2011). Despite their ancestral anti-social behavior, a variety of societal forms have evolved, from facultative aggregations of mostly independent webs, to families of mothers and young, to multiple adult groups that cooperate in a variety of tasks. These societies have evolved multiple times across highly diverged lineages, making the spiders an excellent model system with which to study social evolution.

In the past 15 years, there have been several excellent reviews of spider social behavior. These have focused on colonial behavior, also termed 'communal' under Wilson's (1971) terminology for social insects or 'territorial permanent-social' by Avilés (1997), in which spiders construct webs in tandem, share support threads, but show little direct interaction (Uetz & Hieber 1997; Whitehouse & Lubin 2005; Lubin & Bilde 2011). Reviews have also focused on the 'cooperative' spiders, also termed

‘quasisocial’ (Wilson 1971) or ‘non-territorial permanent-social’ (Avilés 1997), in which spiders mingle within a single web, cooperate in nest construction, prey capture, and parental care, and often forgo dispersal so their life cycle has no obligate solitary phase (Avilés 1997; Whitehouse & Lubin 2005; Lubin & Bilde 2007; Lubin & Bilde 2011). However, there has been no corresponding review of the ‘non-territorial periodic-social’ or ‘subsocial’ (Wilson 1971) spiders, in which groups are composed of single mothers and their offspring that disperse prior to independent reproduction. Subsocial spiders have been incorporated into the reviews of cooperative spider sociality, primarily in evaluating the ‘subsocial route’ to sociality, in which the gregarious phase of subsocial spiders is extended until the solitary phase is completely eliminated (Avilés 1997; Whitehouse & Lubin 2005; Lubin & Bilde 2007; Lubin & Bilde 2011); however, the last reviews to extensively cover subsociality and maternal care in spiders are by Krafft and Horel (1980), Buskirk (1981), and D’Andrea (1987).

This review fills this literature gap and has two primary goals. One, by gathering the literature, particularly of the past 30 years, and summarizing the diversity subsocial and maternal behavior in spiders, we hope to provide a tool for researchers in this and related fields. Two, we hope to push the science forward by synthesizing the literature, evaluating how spiders inform our understanding of the evolution of subsocial behavior, and identifying promising areas of future research.

Maternal care, transient subsociality, and prolonged subsociality

We restrict the focus of this review to what we define as ‘prolonged subsocial,’ or just ‘subsocial’ behavior for simplicity, which we must differentiate from what we term ‘transient subsocial’ (sensu Rayor & Taylor 2006). Trivers (1972) defined parental investment as any investment by the parent that increases the offspring’s chance of survival at a cost to the parent. Under this definition, all spiders show maternal care by investing in eggs and wrapping their eggs in a protective silk case (Foelix 2011). In addition, it is common in many spider families to guard the egg sac and the newly emerged spiderlings for up to one molt (Bristowe 1971; Foelix 2011), which we term ‘transient subsocial.’ Wilson (1971) defined subsocial to include species in which ‘adults care for their own nymphs or larvae for some period of time’ (pg 4), thus excluding species that only exhibit egg care, but otherwise making no restrictions on the duration or complexity of social interactions. This contrasts with Agnarsson et al. (2006a) who restricted subsocial species to those in which the offspring cooperate in some tasks, such as prey capture or expansion of the web. While this definition correctly emphasizes the role of cooperation in defining societies, it runs into the practical problem that many species have not been observed in sufficient detail to confirm cooperative behavior, and often cooperation is simply assumed (Kim et al. 2005a; Lubin & Bilde 2007). Instead, for the purposes of this review, we have adopted a practical, taxon-specific definition for subsociality. We define subsocial spiders as those in which offspring stay together with the parent beyond the age at which they begin to feed, but disperse prior to egg laying and display no alloparental care among adults.

This definition has several advantages. (1) It excludes species displaying only transient subsocial behavior, as typically maternal care ends and the offspring disperse as soon as they begin to feed in these species (Bristowe 1971; Foelix 2011). (2) The molt to the feeding instar is a critical point for spiders because it inaugurates competition for prey and the threat of filial cannibalism and therefore marks a significant hurdle to the evolution of group living. (3) Most references to maternal care in spiders are sufficient to determine if offspring have begun to feed in the natal nest. (4) It excludes the more complex cooperative spider societies that have been reviewed elsewhere.

Even this practical definition generates some ambiguity, however. Several spider species are known to feed on eggs within the egg sac (Valerio 1974). Here, we do not consider feeding within the egg sac as subsocial behavior. We also include species that have previously been considered cooperative or permanent social because they mate within the natal nest prior to dispersal and egg laying (i.e. *Diaea socialis* and *Di. megagyna*; Avilés 1997) and species in which some individuals may forgo dispersal but such behavior is facultative (i.e. *Anelosimus studiosus* and *An. jabaquara*). These species are specifically discussed as transitional species below. Finally, we also note that some species do not fit well into any social category. In the orb-weaver, *Eriophora bistriata*, siblings from a single clutch maintain individual orbs in close proximity to one another and capture most prey individually, but spiders also occasionally cooperate in prey capture, which is necessary for the capture of large prey items (Fowler & Diehl 1978). However, there is no maternal care, as the mother disappears prior to egg hatching (Fowler & Diehl 1978), and therefore the system is not subsocial in the

traditional sense (Wilson 1971). We do not consider *Eriophora bistriata* to be subsocial under our definition, as the absence of maternal care suggests a separate evolutionary path to group living.

In addition to reviewing prolonged subsocial behavior, we also briefly review transient subsocial behavior in spiders to provide background and contrast to longer lasting groups. However, because these behaviors are quite common in spiders, we make no attempt to exhaustively review all spiders in which egg guarding and maternal care of early instars occurs.

Transient subsocial behavior

Transient subsocial behavior takes three forms: egg sac guarding, opening the egg sac, and guarding the first instar out of the sac. Egg sac guarding is common in many families, including Lycosidae, Pisauridae, Oxyopidae, Salticidae, Theridiidae, Scytodidae, Pholcidae and several mygalomorph families (Bristowe 1971; Eberhard 1974; Krafft & Horel 1980; Bowden 1991; Agnarsson 2004). In some cursorial spiders, females hold the sac in their chelicerae (Pisauridae) or attach the sac to their spinnerets (Lycosidae). Others construct a small silken retreat, often in a leaf, under bark or in a similar space (Salticidae, Sparassidae, Clubionidae; Thomisidae). The egg sac is usually laid in or near the web of web-building species (Bristowe 1971). The primary function of egg sac guarding appears to be the reduction of egg sac predation. Eberhard (1974) witnessed *Lyssomanes* females aggressively repelling ants while guarding their eggs, and several removal experiments have shown that most egg sacs disappear if the mother is removed (Fink 1986; Gillespie 1990; Ruttan 1991; Li et al.

1999; Horel & Gundermann 1992; Viera & Romero 2008). In *Stegodyphus lineatus*, females defend their eggs against infanticidal males that do not eat the eggs, but rather destroy them so that the female must lay another sac with his sperm (Schneider & Lubin 1997a). It has also been suggested that tending the egg sac may rid the eggs of fungal parasites (Horel & Gundermann 1992; Li et al. 1999; Li 2002), but it is unclear how the mother prevents the fungus from growing. Egg parasites are common in several species (Fink 1986; Downes 1992; Rienks 2000), and Fink (1986) found that egg guarding had no impact on the presence of mantispid parasites, though whether this is a general pattern awaits studies on additional species. In addition to these biotic threats, females may move the egg sac to regulate its temperature, which may be critical to successful hatching (Norgaard 1956; Bristowe 1971; Willey & Alder 1989; Ruttan 1991).

In several species, mothers end the egg guarding phase by opening the egg sac (e.g. lycosids and theridiids; Krafft & Horel 1980; Stiles & Coyle 2001), and in some cases, spiderlings become trapped and die if the mother is removed from the sac (Willley & Alder 1989; Viera et al. 2007a). The cues mothers use to open the sac at the proper time may derive from spiderlings within the egg sac, hormonal changes within the mother, or some combination of the two (Viera et al. 2007a). Interestingly, this behavior does not seem to correlate well with overall social behavior, as some species with very long social periods and cooperative species do not open the egg sac for their young (Christensen 1984; Downs 1992). There have been no studies on the ecological significance of opening the sac: why some lineages must open the sac and others not, whether the sac is exceptionally thick in species requiring maternal opening, or whether

these sacs afford greater protection against biotic or abiotic threats. All of these questions are worth investigation.

After emergence from the egg sac, it is common for spiderlings to remain together for up to one instar without feeding. The offspring of wolf spiders are well known for riding on their mother's abdomen (Higashi & Rovner 1975). The Pisauridae are also called 'nursery web spiders' for their habit of constructing a small silken nest for their egg sacs and early instar young (Bristowe 1971). Pholcid spiderlings can stay in the natal web for up to two weeks before molting and gradually dispersing (Bristowe 1971). A few studies have examined the function of this short gregarious phase and whether the attractive cues are generated by the mother, the natal nest, or other spiderlings. Fink (1986) found that spiderlings stayed at the natal nest longer if the mother was present, and Willey and Alder (1989) found that young spiderlings suffered lower predation with the mother present.

Distribution of subsocial behavior

Our search of the literature revealed 60 species considered to be subsocial under our definition (Table 1). In addition to species listed on Table 1, all 17 species of *Stegodyphus* are believed to be subsocial or social (Ruch et al. 2009a), bringing the total number of species to 71. It is also probable that many more of the more than 50 species of *Anelosimus* are also subsocial (Agnarsson & Kuntner 2005; Agnarsson 2006). Our count brings the total up considerably from recent estimates that vary from about 20 (Whitehouse & Lubin 2005; Foelix 2011) to 30-40 (Coddington & Agnarsson 2006). Some species that were previously considered subsocial, e.g. *Achaearanea*

tepidariorum (Avilés 1997; Whitehouse & Lubin 2005) and *Aulonia albinmana* (Whitehouse & Lubin 2005) have been removed because mother offspring associations are short-lived and there is little evidence that spiderlings feed prior to dispersal (Buskirk 1981; Krafft & Horel 1980). We also consider *An. pacificus* subsocial because spiderlings feed on prey captured by the mother (Agnarsson et al. 2006b), while Agnarsson and colleagues have classified this species and its related species as solitary because associations are short and there is no evidence for cooperation among siblings. Undoubtedly, there are many more subsocial species that are yet undocumented. Additionally, although our review is as comprehensive as possible, it is also possible that we missed some references, particularly short natural history notes in the taxonomy literature or non-peer reviewed articles in the pet trade literature.

Despite the gaps in our knowledge, the patterns of subsocial behavior in the spiders have begun to emerge. It has evolved at least 18 times in 16 families (at least twice in the Theridiidae and the Lycosidae and once in every other family on Table 1). Subsociality is found in both the basal mygalomorph and the more derived araneomorph spiders. Given that about 95% of all spider species are araneomorphs (Platnick 2011), it is unsurprising that most examples of subsociality are also found in this infraorder. Some families appear to be phylogenetic hot-spots, where subsocial species have either repeatedly evolved or have greatly proliferated. This is case in the Theridiidae and the Eresidae. Maternal care appears to be ancestral in the theridiid 'lost colulus clade' consisting of the genus *Anelosimus* and the Theridiinae (including genera *Achaearanea*, *Theridion*, *Chrysso* and *Helvibis* on Table 1) and includes hundreds of species (Agnarsson 2004). Maternal care and subsociality also arose in

the phylogenetically distant genus *Latrodectus* (Bertani et al. 2008), suggesting at least two origins of subsociality in this family. Whether or not maternal care evolved independently in *Argyrodes* is uncertain, as *Argyrodes* is phylogenetically close to the lost colulus clade, and maternal care and kleptoparasitism (common in *Argyrodes*) may be interrelated (Agnarsson 2002, 2004). All eresids studied to date show extensive maternal care (Schneider 2002), suggesting a great proliferation of maternal care in this family. Although only documented in 4 species, subsociality probably arose twice in the Lycosidae, once in the web-building Sosippinae (*Sosippus* and *Aglaoctenus*) and once in the more distantly related *Geolycosa* (Murphy et al. 2006). There are conspicuous absences, as well, most notably the ecribellate orb-weavers (but see *Eriophora bistriata* discussed above). The orb-weaving families, Araneidae, Tetragnathidae, and Nephilidae, together include more than 4,000 species, many of them conspicuous and well-studied, yet they have no subsocial species. This may be because only one spider can effectively use the structure of the orb web (Avilés 1997). Subsocial behavior has evolved in the cribellate orb-weaving spider *Philoponella congregabilis*, but here the orb appears much reduced, and the majority of the web is a 3-dimensional mesh (pers. obs.). There are also no subsocial species in the Linyphiidae, which, with over 4,400 species, is the second most speciose spider family. The linyphiids usually spin sheet webs, not unlike many subsocial species, making the absence of subsociality in this family curious. Perhaps subsocial behavior in these mostly very small spiders has simply been overlooked.

Who cares?

All known cases of parental care in spiders are, without exception, maternal. The absence of paternal care in spiders supports the theory that internal fertilization promotes maternal over paternal care because the time between mating and egg laying allows the male to desert the offspring first (Ridley 1978) and also makes the male's parentage uncertain (Ridley 1978; Queller 1997). Simply the absence of the male is not by itself a sufficient explanation for the absence of paternal care in spiders, however. In many of the cooperative species that forgo dispersal, males are retained in the colony at the same time as offspring, yet they perform few activities other than mating (Avilés 1997). Similarly, males can be adept at securing their paternity (e.g. mate plugs Uhl et al. 2010), yet this is insufficient to evolve paternal care. Two additional barriers may make the evolution of paternal care unlikely. One, males often die shortly after mating (Gillespie 1990; Marques 1998; Bilde et al. 2002; Foelix 2011), and may not even feed as adults (Buchli 1969). Therefore, males may be physiologically and behaviorally ill-equipped to guard and provision young for any length of time. Two, in nearly all spiders, males search for mates while females are often sedentary (Schneider & Andrade 2011). The maintenance of male territories, in which females lay their eggs, is thought to promote the evolution of paternal care in the arachnid order, opiliones (Machado & Raimundo 2001). However, such a mating system has only been documented in the wolf spider *Allocosa brasiliensis*, and the male leaves his burrow after mating, providing no further care for his offspring (Aisenberg et al. 2007). We note that there has been one report of paternal care in a pisaurid by Walckenaer (cited in Buskirk 1981); however, we have been unable to find any corroborative evidence for

this account. It seems likely that the nuptial gift wrapped in silk and carried by the male (Stålhandske 2002) was mistaken for an egg sac.

While our definition of subsociality excludes alloparental care by adults, alloparental care by immature siblings may be present in some species. Whether one sibling directly cares for another, whether siblings benefit through mutual cooperation, or whether siblings exploit each other are all possible interactions. We discuss these issues below.

The function of subsocial behavior I: Benefits derived from the mother

Parental investment, by definition, enhances offspring fitness. We examine the mechanisms by which offspring benefit from subsocial behavior of the mother, which we divide into three categories: provisioning, defense against predators and parasites, and the nest that was either created or secured by the mother.

Mothers provision their young by sharing prey, regurgitation, trophic eggs, or matriphagy. Of these, sharing prey or dropping prey and allowing the young to feed is by far the most common (Table 1). Prey sharing is probably the ancestral form of provisioning in most lineages, not only because it is common, but also because it requires no significant behavioral or physiological modification in the female. She simply continues to capture prey, as she would without offspring, but relinquishes part of her meal, and not always willingly (see Gundermann et al. 1988; Downes 1992; Curtis & Carrel 1999; Yip & Rayor 2011 for cases when the mother attempts to repel juveniles from her prey). While in some species, prey sharing by the female may be quite passive, in other species, mothers communicate the presence of food to their offspring,

i.e. *Achaearanea riparia* (=*Theridion saxatile*) (Norgaard 1956), *Anelosimus crassipes* (Ito & Shinkai 1993) and *Ischnothele caudate* (Jantschke & Nentwig 2001). Likewise, juveniles may also signal to the mother. In *Coelotes terrestris*, solicitation behavior by the young prompts the female to drop the prey and spend less time feeding on it herself (Gundermann et al. 1988). Sharing prey seems to have been lost or never evolved in the Eresidae, in the miturgid, *Cheiracanthium japonicum*, and in the amaurobiid, *Amaurobius ferox*, all of which also have obligate matriphagy. In *Stegodyphus*, females cease capturing prey after eggs hatch, and provision their young entirely through regurgitation until they are consumed by their offspring (Kullmann & Zimmermann 1974; Salomon et al. 2005). There are conflicting reports on whether *Eresus cinnaberinus* mothers continue to feed during brood care (see Kullmann & Zimmermann 1974; Johannesen et al. 1998), but she feeds the young by regurgitation (Johannesen et al. 1998). In *Ch. japonicum*, the spiderlings' first meal is the body of their mother (Toyama 2001), and in *Am. ferox*, offspring only feed on trophic eggs before consuming their mother (Kim & Roland 2000).

Regurgitation is ubiquitous in eresids and common in the theridiids (Table 1). It has also evolved once in the lycosids (Stefani et al. 2011) and once in the uloborids (cited in Downes 1995). Kullmann and colleagues first conclusively demonstrated regurgitation in spiders by feeding spiders flies with radioactive isotopes (Kullmann 1972; Kullmann & Zimmermann 1974). Few studies have examined the composition of the regurgitate, but in *Stegodyphus*, it appears to consist of digested food, the dissolved gut epithelium, and fat tissue. (Salomon et al. 2005). In *Theridion sisyphium* and *Th. impressum*, the regurgitate is produced by intestinal cells (Kullmann 1972). No studies

have examined why regurgitation evolved in preference to sharing prey, but in species in which both prey sharing and regurgitation occur, regurgitation is restricted to the early instars, while older offspring share prey with the mother (Kaston 1965; Brach 1977; Marques et al. 1998; but see Whitehouse & Jackson 1998 for when regurgitation and prey sharing can both occur in the same instar). Theridiids and eresids also leave much of their prey intact while feeding (Bristowe 1971; Lubin & Ward 1993), so that very young spiders may have difficulty sharing prey if they must pierce the prey's cuticle to create a feeding site. Alternately, regurgitation may ensure that young spiders are fed in environments where prey capture is uncertain.

While consumption of eggs within the egg sac is fairly common in spiders (Valerio 1974; Kim & Roland 2000), the production of trophic eggs for juveniles outside the egg sac is rare and has only evolved three times: in the amaurobiids, agelenids, and thomisids. In both *Amaurobius ferox* and *Coelotes terrestris*, trophic egg laying occurs early in juvenile development. In *Am. ferox*, it is the first meal for spiderlings (Kim & Roland 2000). In *Co. terrestris*, the female lays a second clutch soon after the first, but most eggs do not develop and instead serve as food (Horel & Gundermann 1992; Trabalon & Assi-Bessekon 2008). *Co. terrestris* appears to lay a second round of trophic eggs that are laid individually or seized directly from the genital opening by juveniles (Gundermann et al. 1991). Trophic eggs can account for 25% of the mother's mass in *Am. ferox*. She also appears to signal that she is about to lay trophic eggs to her young by drumming her palps (Kim & Roland 2000). In the thomisid, *Diaea ergandros*, the trophic eggs develop from ovaries modified after fertile egg laying. These eggs are too large to be laid and do not stain for nuclear material. They are

retained within the female and eaten as the offspring consume her (Evans et al. 1995). No species both regurgitates and lays trophic eggs, suggesting that both forms of provisioning may serve the same purpose in providing accessible and/or dependable food for very young offspring.

Matriphagy may be obligate or facultative. Obligate matriphagy occurs in all studied eresids (Schneider 2002), *Amaurobius ferox* (Kim & Horel 1998), *Diaea ergandros* (Evans et al.1995), *Theridion impressum* (Kullmann 1972), and possibly *Th. japonicum* though the sample size was small for this species (Ito 1985). Additionally, matriphagy occurs occasionally in *Anelosimus arizona* (Avilés & Gelsey 1998), and under starvation conditions in the laboratory in *Coelotes terrestris* (Gundermann et al. 1997). In all cases, spiders are semelparous (Table 1). While matriphagy is often described as an 'extreme' form of parental care (Evans et al. 1995; Foelix 2011), it is not so surprising that mothers would sacrifice their bodies to their offspring when future reproduction is limited (Schneider & Lubin 1997b; Kim et al. 2000). What is more surprising is that matriphagy is not more common, given that in many other species, mothers die either in the presence of their offspring or soon after they disperse (Brach 1976; Brach 1977; Miller 1989; Gillespie 1990; Downes 1992; Pourié & Trabalon 1999; Yap & Li 2009). The rarity of matriphagy may be due to the sophisticated interaction required between juveniles and mother. While in some species in which matriphagy is facultative, i.e. *Co. terrestris*, the juveniles may overpower the mother while she attempts to escape (Gundermann et al. 1997), in species with obligate matriphagy, the process requires mutual coordination between parent and offspring. In *Am. ferox*, the mother increases her activity and web vibrations leading up to matriphagy, while the

juveniles increasingly gather and eventually swarm on top of her (Kim & Horel 1998). When mothers were experimentally placed with young of different ages, matriphagy occurred later and was less coordinated, with fewer spiderlings swarming the mother. Juveniles that had already fed on their mother did not eat their foster mother, suggesting that both internal and external signals are required for matriphagy (Kim & Horel 1998).

It is presumed that provisioning by the mother enhances survival, growth, and development of the offspring. This has been explicitly studied in several species. *Coelotes terrestris* spiderlings had better survival and gained more weight than orphaned spiderlings (Gundermann et al. 1991; 1997). *Amaurobius ferox* spiderlings had higher survival and molted earlier when they could feed on the mother and trophic eggs (Kim & Roland 2000; Kim et al. 2000). *Cheiracanthium japonicum* spiderlings deprived of their mother as their first meal dispersed earlier and at one-third the size than if they had fed on her (Toyama 2001), and orphaned *Phryganoporus candidus* juveniles suffer over 9 times the mortality rate as those kept with their mother (Downes 1992). However, all of these studies have been conducted in the laboratory, which may overestimate the importance of the mother if spiderlings can capture more of their own prey under field conditions. Evans (1998a) compared field colonies that had the mother removed to those that did not. He found that the size of spiderlings between treatments did not differ but that colonies without mothers usually did not persist, partly because juveniles abandoned the nest (Evans 1998a).

The second function of maternal care is the defense of the brood against predators and parasites. Due to the difficulty of field observations, few studies have

documented maternal defense against predators. However, *Argyrodes flavipes* mothers were observed chasing away conspecifics in the field (Whitehouse & Jackson 1998). *Coelotes terrestris* mothers defend their eggs from oophagic conspecifics in laboratory introductions (Horel & Gundermann 1992). Yip and Rayor (2011) introduced potential predators into field retreats of *Delena cancerides* and found that mothers chased out and killed predators, while offspring (even large offspring) ignored or ran from predators. More commonly, researchers have inferred maternal defense by removing mothers from nests and recording a decrease in juvenile survivorship (Gillespie 1990; Schneider & Lubin 1997b; Jones & Parker 2002; but see Ruttan 1991 for no change in survivorship). Little work has been done on the role communication may play on predator defense in spiders, but *Achaearanea riparia* mothers seem to generate web vibrations that repel juveniles, suggesting that females may warn their brood of predators or other danger (Norgaard 1956).

Finally, in some species, the end of group living coincides with the cessation of maternal care, for example *Theridion pictum* (Ruttan 1991), *Theridion grallator* (Gillespie 1990), and *Cheiracanthium japonicum* (Toyama 2001) (Table 1). However, in many species, the juveniles remain in the natal nest after the death of the mother, and several authors have suggested that this is because the nest itself is a valuable resource for the spiders (Evans & Main 1993; Rienks 2000; Kim 2005). Silk is quite costly to produce, and young spiders may save energy by using pre-existing webs (Jakob 1991). This may be the case in the eresids, *Amaurobius ferox*, and the three species of subsocial *Diaea*. Whether spiders remain in the natal nest due to benefits from siblings (see below) or from the nest itself has only been examined in a few

species. In *Am. ferox*, siblings capture prey more quickly in webs inherited from their mother than in webs constructed by the siblings (Kim 2005). In *Diaea socialis*, the maternal period is relatively short, only 4-5 weeks, while the offspring remain in the natal nest for an additional 18 months (Evans & Main 1993), suggesting considerable benefits beyond the presence of the mother. Further, it is the web itself that is attractive to pre-reproductive spiders (Evans & Main 1993). In *Delena cancerides*, the bark retreat is secured with a minimal amount of silk and therefore not costly to construct. However, bark retreats are quite rare and competition for them can be intense, suggesting that spiders remain in the natal nest without their mother due to habitat saturation (Rayor et al. in prep.; Yip & Rayor in prep., see Chapter 5).

The function of subsocial behavior II: Benefits derived from siblings

Because spiders are always born in a group (Foelix 2011), subsocial behavior allows offspring to interact with and possibly benefit from their siblings. The three areas in which spiders are known to cooperate are in prey capture, nest construction, and brood care (Avilés 1997). By our definition, all siblings are pre-reproductive, so brood care is eliminated as a possibility, leaving cooperation in nest construction and prey capture as possibilities.

Offspring begin to enlarge and repair the web as they mature in the social crab spider genus *Diaea* (Evans & Main 1993; Evans 1998a), *Phryganoporus candidus* (Downs 1994), *Anelosimus jabaquara* (Marques et al. 1998), *Kukulcania hibernalis* (Curtis & Carrel 1999), *An. studiosus* (Brach 1977), and *Amaurobius ferox* (Kim et al. 2005b). This is probably also true for any web building species in which juveniles

remain in the natal nest long enough to exhibit their own predatory (and therefore snare building) behavior. While the nest expands with group size, the per capita silk expenditure declines with group size, so that each spider is paying a smaller cost (Evans 1998a). A larger web has a larger surface with which to intercept and capture prey (Evans & Main 1993; Yip et al. 2008). A larger web has also been shown to better protect the residents from predation (Evans 1998a).

As offspring age, they also begin to capture prey without their mother, and they often cooperate in prey capture and share prey with siblings. Cooperative prey capture allows spiders to capture prey larger than what they could subdue alone (Jones & Parker 2000, 2002; Kim et al. 2005b; Yap & Li 2009), and they can capture prey faster (Kim et al. 2005b). Whether this increase in prey availability can compensate for prey competition among siblings has only been investigated in a few species. Under greenhouse conditions, *Anelosimus studiosus* spiderlings kept in groups obtained more food per capita than single spiders (Jones & Parker 2000). However, per capita prey capture within colonies (i.e. > 1 spider) decreased with colony size and there was no difference in growth rate between grouped and single spiders (Jones & Parker 2000). Under field conditions, single *An. studiosus* spiders could develop well if they captured any prey at all, but most did not and starved at greater rates than spiders kept with their siblings and mother (Jones & Parker 2002). Under a laboratory feeding regimen, *Stegodyphus lineatus* spiders were smaller and had higher mortality in colonies with more spiders (Schneider 1995). In many species, spiders that do not participate in prey capture still get to feed (Kim et al. 2005a), and may even have better access to nutritive feeding sites than attacking spiders (Kim et al. 2005a) or steal the prey away from the

capturing spider (Kim et al. 2005b). This opens the possibility that spiders may cheat, i.e. let siblings absorb the cost of attacking prey and risking injury, while reaping the benefits of feeding on the prey. How cheating is kept in check, allowing societies to persist, requires further investigation.

Few subsocial spiders produce successive egg sacs, so that offspring are the same age (Table 1). Age (and therefore size) variation among siblings creates asymmetries that might lead to more complicated dynamics, such alloparental care or exploitation. For example, when dominance hierarchies are applied to the 'producer-scrounger' model, it was predicted that more dominant individuals would adopt the scrounger tactic and usurp less dominant individuals' prey (Barta & Giraldeau1998). Conversely, older siblings may provide food to younger siblings, as is common in the cooperatively breeding birds (Hatchwell 2009), mammals (Riedman 1982), and fish (Wisenden 1999). It has been suggested that developmental homogeneity facilitates cooperation in spiders (Schneider 1995; Kim et al. 2005a), but it seems that this is not a general rule. Greater size variation within the single clutch increased mortality in groups of *Stegodyphus lineatus* (Schneider 1995) and rates of aggression in *Hysterocrates gigas* (Varrecchia et al. 2004). However, it was reported that larger offspring in *Anelosimus jabaquara* (also with predominantly one clutch) feed smaller siblings (Marques et al. 1998). Offspring of multiple ages cohabiting in the natal nest are found in *An. beaza* (Avilés et al. 2001), *An. kohi* (Agnarsson & Zhang 2006), *Ischnothele caudate* (Jantschke & Nentwig 2001), *Delena cancerides* (Rayor et al. in prep.), *Phryganoporus candidus* (Downes 1993), and *Menemerus bracteatus* (Rienks 2000). Of these, the impact of older siblings on younger spiders has only been investigated in *I.*

caudate, *P candidus*, and *D. cancerides*. *Ischnothele caudate* subadults tolerated younger spiders, but did not feed them (Jantschke & Nentwig 2001). It was found that young *P. candidus* spiderlings cannot survive on their own and must have an older 'helper' (Downes 1993). Paradoxically, this helper often cannibalizes its young dependent, but the average effect seems to be positive for the younger spider (Downes 1993). In *D. cancerides*, younger spiders are heavier in the presence of older siblings, and the transfer of resources from older to younger siblings (e.g. by prey sharing) seems the most likely explanation (Yip & Rayor in review, Chapter 4).

Costs to the mother

It is assumed that parental care entails a loss of future reproduction to the parent. This is generally true in spiders. In every species in which it has been examined, spiders will produce additional egg sacs if their previous egg sac is removed (Fink 1986; Gundermann et al. 1997; Marques 1998; Kim et al. 2000; Toyama 2003). There is also a general trend for fecundity to decrease with social level (Krafft & Horel 1980; Buskirk 1981), suggesting a physiological trade off between producing offspring and caring for them. The reduction in both egg and egg sac production may reflect a decrease in maternal resources that she instead gives to her offspring. The second deposition of yolk into the eggs is dependent on food resources (Foelix 2011), so there is a direct trade off between food given to current offspring and yolk given to future offspring. In *Coelotes terrestris*, females kept with their offspring lost significantly more weight than those separated from their offspring under identical conditions (Gundermann et al. 1991). *Stegodyphus lineatus* mothers lose 41% of their weight to regurgitation before

allowing their offspring to eat them (Salomon et al. 2005), and *Sosippus floridanus* mothers rarely feed themselves and instead give all their prey to their offspring (Brach 1977). While these studies demonstrate that maternal care usually depletes maternal resources, one study on *Anelosimus studiosus* showed that adult females with offspring survived longer and produced second egg sacs sooner (though most females produced only one sac) than females that had their brood removed (Jones & Parker 2002). Females may benefit from older offspring that cooperate in capturing prey and enlarging the web (Jones & Parker 2000, 2002), so in the later stages of offspring development, parental care may actually act a mutualism, benefiting both parent and offspring. Because any benefit to the mother is restricted to the latter stages of offspring development, benefits to the mother may play a role in the extension of maternal care but not in its initial evolution.

It has been shown in cooperative social and colonial species that larger nests attract more predators and parasites (Uetz & Hieber 1997; Avilés & Tufiño 1998), so the female may also incur a survival cost by remaining with her offspring. However, whether the patterns seen in the colonial and social species also hold true for subsocial species, that usually produce a much smaller range of colony sizes, has not been tested. Downes (1992), for example, provided a detailed list of predators and parasites of *Phryganoporus candidus*, but did not relate their frequency with colony size. Kleptoparasites become more common as the colony develops in *Anelosimus jucundus* (or *baeza*, see Agnarsson 2006), so females may incur the cost of having their food stolen by unrelated species by staying with their offspring (Nentwig & Christenson 1986). One study found no survival cost to egg sac guarding in the oxyopid, *Peucetia*

viridans (Fink 1986), but no other studies have examined the cost of predation to subsocial spider mothers.

Kin recognition

Spiderlings derive significant benefits from their mother, as well as from siblings, and in exchange, the mother may suffer significant costs. If spiders come into contact with non-kin, it is expected that kin recognition should evolve so that the beneficiaries of costly behavior are genetic relatives. Spiders have been observed to immigrate into foreign nests in *Theridion grallator* (Gillespie 1990), *Diaea ergandros* (Evans 1998b; Evans & Goodisman 2002), and *Delena cancerides* (Rowell & Avilés 1995; Yip et al. 2012). However, early studies comparing kin and non-kin interactions in subsocial groups did not detect any kin recognition (Krafft & Horel 1980). Unrelated juveniles introduced into the group were tolerated by both the mother and her offspring (Brach 1976, 1977; Miller 1989; Gillespie 1990; Trabalon et al. 1996). Unrelated mothers placed in the nest began to feed their adopted offspring as they would for their own progeny (Ito 1985; Kim & Horel 1998). Mothers may even feed the spiderlings of other species, as is the case in *Theridion sisyphium* (Kullmann 1972). However, there has been a steady accumulation of evidence that many species do recognize kin. *Anelosimus crassipes* adult females either recognize their own young or their own silk, as they ran away from foreign webs with foreign offspring (Ito & Shinkai 1993). More often kin recognition by spiders is more subtle, and differential behavior may only manifest under certain conditions. *Diaea ergandros*, *Stegodyphus lineatus*, and *D. cancerides* juveniles were all more likely to cannibalize unrelated spiders than kin, but

only under conditions of food stress (Evans 1999; Bilde & Lubin 2001; Beavis et al. 2007). When provided with ample prey, *D. cancerides* spiders showed no preference for cannibalizing unfamiliar conspecifics; however, they were more investigative toward unfamiliar spiders (Yip et al. 2009). *Diaea ergandros* mothers may not cannibalize foreign juveniles, but they appear to feed them less than their genetic offspring (Evans 1998b).

The mechanism of recognition has not been fully explored although cuticular cues are probably involved (Trabalon & Bagnères 2010). The social spider, *Stegodyphus sarasinorum*, can differentiate between prey and conspecifics by contact alone (Kullmann 1972). Disrupting the sensory appendages (legs and palps) with HCl increased aggression in wolf spiders, as did painting liquefied fly viscera onto the cuticle (Miller 1989). The cuticular compounds have been cataloged in *Tegenaria atrica* and molecular profiles change in accordance with changes in aggressive behavior (Trabalon et al. 1996; Pourié & Trabalon 1999). Chemicals on the web may also serve as recognition cues. *Coelotes terrestris* juveniles are attracted to their mother's silk over unrelated females', but only during their gregarious phase (Trabalon & Assi-Bessekon 2008). Young juveniles also prefer the silk of maternal spiders to virgin females, and chemical signature of the silk appears to change with female reproductive state (Trabalon & Assi-Bessekon 2008). *Stegodyphus lineatus* spiders recognize their own silk, and prefer it when well-fed, but show no preference for the silk of kin or non-kin (Bilde et al. 2002).

Ecology, life history, and the evolution of subsociality

According to parental care theory, parental care is likely to evolve when young face harsh environments, high rates of predation, and high competition (Clutton-Brock 1991). Certainly this fits with the observed benefits that spiderlings derive from maternal care, particularly obtaining food and protection from predators from the mother. The logical prediction is that subsociality in spiders should evolve in environments where predation pressure is particularly high and where young spiders are unlikely to find prey, perhaps in environments with relatively low abundance of small prey items. However, no such cross species analysis exists. A detailed analysis comparing the habitats of subsocial species and their transient subsocial relatives is beyond the scope of this review. However, it is clear that subsocial spiders are capable of inhabiting a wide variety of habitats including deserts, tropical rain forests, temperate deciduous forests, dry sclerophyll forests, and dry steppe grasslands (Table 1).

There is a strong latitudinal pattern in the distribution of social behavior in spiders, with more social species at lower latitudes (Avilés 1997). An analogous pattern within the subsocial spiders, using the duration of association as a measure of sociality, appears much weaker (Fig. 1). Several species with short association periods, such as *Anelosimus pacificus* in Costa Rica (Agnarsson 2006b), and *Argyrodes flavipes* in tropical northern Australia (Whitehouse & Jackson 1998), live at low latitudes. While some species that remain in groups for a year or more (*An. studiosus*) or at least to the sixth molt (*Eresus cinnaberinus*) live at fairly northerly latitudes. Subsocial species are found as far north as Denmark (*Achaearanea riparia*), northern Minnesota USA (*Theridion pictum*), and Hokkaido Japan (*Cheiracanthium japonicum*); however, these northernmost species remain in groups for about a month or less (Fig 1). It appears

that species that live together for a year or more (or to maturity) are absent at very high latitudes and environments with harsh winters, with their most extreme latitudes in near Washington DC, USA (*An. studiosus*; Agnarsson 2006a) and Tasmania, Australia (*Delena cancerides*, *Diaea ergandros*), where sustained periods of subzero temperatures are rare. How harsh winters might disrupt social groups is unclear, as some otherwise solitary species overwinter in groups (e.g. *Paraphidippus marginatus*, *Coriarachne versicolor*; Buskirk 1981). It could be that, while high latitude habitats can support groups of young spiders, the prey requirements of groups of spiders near adulthood cannot be met. This is similar to the argument proposed to explain the gradient between social and subsocial spiders in the genus *Anelosimus* (Avilés et al 2007; Powers & Avilés 2007); however, more evidence is needed to examine this hypothesis as it applies to the distribution of subsocial spiders.

Simple characteristics of the environment alone are insufficient to explain the evolution of maternal care. There is no environment, no matter the predation pressure or prey abundance, in which all spider species display maternal care, and in any given environment, most species are solitary. Indeed, if maternal care and subsociality evolved to cope with low juvenile survival by reducing starvation and predation, an equally, if not more, parsimonious solution to the same problem is to increase reproductive output. In other words, why do some species opt for the low fecundity-high survival strategy over the high fecundity-low survival strategy, when both strategies may result in similar fitness in the same environment? This question of why sociality arises in some lineages and not others is an ongoing debate in the insects and vertebrates, as well (Arnold & Owens 1999; Tallamy & Brown 1999; Hatchwell 2009). Part of this

difficulty may arise from the complex interactions between environment and life history traits (Arnold & Owens 1998; Arnold & Owens 1999; Hatchwell & Komdeur 2000). To understand the evolution of sociality, the various traits of the system, both intrinsic to the animal (life history traits) and extrinsic (environmental traits) must be considered in concert.

One life history characteristic that may promote the evolution of subsociality is semelparity. Organisms should invest in greater parental care for terminal reproductive bouts because there is little cost to future reproduction (Clutton-Brock 1991). As an extreme form of this, semelparity may promote the evolution of parental care because parental care carries no cost to future reproduction (Tallamy & Brown 1999). Most spiders are iteroparous (Bristowe 1971). However, of 39 subsocial species, for which there is some egg sac data, 27 produce only a single egg sac under field conditions (Table 1). While there appears to be an association between semelparity and maternal care in spiders, it is unclear which preceded the other. As discussed above in the context of costs to the mother, many species will produce second egg sacs if the first is removed. Semelparity may then be a consequence of maternal care rather than a cause, at least in some lineages. Schneider and Lubin (1997b) investigated mortality of both juveniles and mothers in *Stegodyphus lineatus* and concluded that maternal care is the better strategy because females rarely survive to the hatching of their second clutch. Further*, Anelosimus studiosus* females in Uruguay can lay up to 6 egg sacs in the laboratory, but usually only lay one in the field (Viera et al. 2007b), suggesting that females' resources are restricted in the field. Thus, predation pressure and food

limitations on adult females, and not just juveniles, may also lead to the evolution of maternal care by promoting semelparity.

Another life history trait is use of a permanent nest. There is one account by Avilés et al. (2001) of juveniles of an unidentified sparassid moving as a group, but all other subsocial spiderlings remain at a fixed nest until dispersal. Spiders are known to swarm in some of the social species, as a means of group dispersal (Lubin & Robinson 1982), and in one social species, *Aebutina binotata*, entire colonies can migrate tens of meters or more (Avilés 2000). However, in these examples spiders of similar size move as a group, and Avilés (2000) suggested that developmental synchrony may be required for group migration, perhaps making it difficult for mothers and offspring to move together. In any case, it is exceptionally rare for spiders to maintain group cohesiveness over long distances. Given this constraint, we might expect subsociality to be rarer in cursorial lineages (e.g. Lycosidae, Miturgidae, Salticidae, Scytodidae, Sparassidae, Thomisidae on Table 1). This appears to be the case, as only 14 of 60 subsocial species belong to these lineages, when about half of all spider species do (Blackledge et al. 2009). In all cases, these species either construct a silken nest (*Cheiracanthium japonicum*, *Diaea*, *Sosippus*, *Scytodes*), construct a burrow (*Geolycosa turricola*), or live under bark (*Delena cancerides*, *Menemerus bracteatus*).

Finally, mating systems may play a role in the evolution of subsociality via kin selection. As discussed above, cooperative prey capture and nest construction by siblings may mutually benefit all participants, though the system is vulnerable to cheaters (Kim et al. 2005a). Relatedness among group members discourages cheating, and several studies have shown that groups of juveniles cooperate better with

siblings than with unfamiliar spiders. In *Diaea ergandros*, groups of siblings spun larger nests than groups of unrelated individuals, which improved survival in intermediate sized groups (Evans 1999). More recently, it was shown that both *Stegodyphus lineatus* and *St. tentoriicola* juveniles feed more efficiently with kin than nonkin (Schneider & Bilde 2008; Ruch et al. 2009a); however, no effect of kinship was found in a similar experiment in *Delena cancerides* (Auletta & Rayor 2011). In order for siblings to actively cooperate in prey capture, however, they must already have reached the feeding stage in groups. Active cooperation among siblings (and the possibility of cheating) therefore probably evolved after prolonged maternal care and subsociality, as it is defined here. A more immediate obstacle to group living is the threat of cannibalism. Although cooperation and altruism are usually ascribed to active behaviors, inaction may also be altruistic. Tolerance is a form of altruism, as a spider forgoes a meal by refraining from cannibalizing a sibling (Anthony 2003). Thus tolerance may be a means of maximizing inclusive fitness when surrounded by close relatives.

Whether tolerance evolves will then depend on the relatedness among individuals in the natal nest. Relatedness among siblings will vary depending on the number of fathers of the clutch. Females of several species will readily mate multiply in the laboratory (Marques et al. 1998; Albo et al. 2007; Jones & Parker 2008), but the mating systems of only a few subsocial species has been investigated under field conditions. *Stegodyphus tentoriicola* females encounter only 1.3 males on average during their receptive period (Ruch et al. 2009b). *Stegodyphus lineatus* females received an average of 2.1 visiting males (Schneider 1997), and *Anelosimus arizona*

females mated with an estimated 4.4 males over their lifetime (Klein et al. 2005). However, multiple matings do not necessarily translate to multiple paternity. In *An. studiosus*, there is complete first male sperm precedence in laboratory females mated to two males (Jones & Parker 2008). It is still unknown how multiple matings translate into paternity for most species in the field. The estimated relatedness among subsocial juveniles has only been reported in *Diaea ergandros* and *Delena cancerides*. Mean relatedness within *Di. ergandros* nests was 0.44, significantly lower than 0.5 expected for full siblings (Evans & Goodisman 2002). This was probably due to multiple paternity, although immigration of unrelated individuals may also play a role (Evans & Goodisman 2002). In *De. cancerides* nests, mean relatedness was found to be 0.27, though this was due to the presents of unrelated immigrants (Yip et al. 2012). Relatedness within colonies without detected migrants did not differ from 0.5 (Yip et al. 2012). To test the role of kin selection in the evolution of subsociality, future studies should compare the number of fathers per clutch of subsocial species and their transient subsocial relatives.

Consequences of subsociality I: Dispersal

One proposed consequence of subsocial behavior that has as yet received little attention is that subsocial spiders have relatively limited dispersal (Brady 2007). Many young spiders disperse by ballooning, yet by remaining in the natal nest until they are near adulthood, spiders may forfeit this mode of dispersal, as it is generally only possible for very small spiders (Schneider et al. 2001). Spiders are not known to balloon in *Theridion grallator* (Gillespie 1990), *Amaurobius ferox* (Kim et al. 2005b), or *Sosippus sp.* (Brady 2007). Several subsocial spiders, e.g. *Anelosimus arizona*

(Powers & Avilés 2003) usually disperse very short distances, often within a few meters. *Stegodyphus* is an exception in that adults in this genus are still able to balloon (Schneider et al. 2001). It is still unclear how the multi-stranded silk for ballooning is produced in these spiders, though the cribellum (an ancestral spinning structure that has been lost in many lineages) may be involved (Schneider et al. 2001). Once dispersal is limited, populations can become highly structured and reproductively isolated. Reproductive isolation could lead to greater speciation. Conversely, isolated populations, with limited geographical range, may also be prone to extinction. The wide distribution of some subsocial species, for example *An. studiosus*, argues against the hypothesis that subsociality limits geographic range; however, it was recently argued that *An. studiosus* is a complex of several species (Agnarsson 2006a). It has also been reported that *An. baeza* behaves differently in nearby populations (Agnarsson 2006a), suggesting that some subsocial 'species' may actually be species complexes. Speciation and extinction have been investigated in the permanent-social *Anelosimus* and *Stegodyphus*, which, because there is little migration among colonies, form reproductively isolated demes (Agnarsson et al 2006a; Johannesen et al. 2007). Social species tended to be on the tips of phylogenies, showing either low speciation or high extinction (Agnarsson et al. 2006a; Johannesen et al. 2007); however some species were quite old, showing that sociality is probably not a transient state (Johannesen et al. 2007). Similar studies are lacking in the subsocial spiders, and such studies could focus on predicted differences between ballooning and non-ballooning species.

Consequences of subsociality II: Evolution to a more or less social state

The subsocial route to permanent sociality has been reviewed recently (Avilés 1997; Lubin & Bilde 2007; Lubin & Bilde 2011) and will only be discussed briefly here. With few exceptions (see Agnarsson et al. 2006a), the sister species of the permanently social spiders are subsocial, providing strong evidence that the social spiders have evolved independently many times from subsocial ancestors (Kraus & Kraus 1988; Agnarsson et al. 2006a). In order for sociality to evolve, remaining in the natal nest to mate and brood must have been less costly than dispersing, searching for mates, and independent reproduction. For this to be true, two obstacles need to be overcome: inbreeding depression, and the increased competition that results from multiple breeding adults.

The negative effects of inbreeding can erode over time if individuals with deleterious alleles fail to reproduce, purging these deleterious alleles from the population (Avilés & Bukowski 2006). In two subsocial species with social congeners (*Anelosimus arizona* and *Stegodyphus lineatus*) dispersal distances for both sexes are very short (Avilés & Gelsey 1998; Powers & Avilés 2003; Johannesen & Lubin 2001; Bilde et al. 2005) and mate preference for non-kin is weak or absent (Bilde et al. 2005). Some degree of inbreeding is probably the norm in these species, and the effects of inbreeding are relatively minor (Bilde et al. 2005; Avilés & Bukowski 2006) and may be entirely masked by cooperation (Avilés & Bukowski 2006). These are the two species most studied with regard to dispersal and inbreeding, but short dispersal distances have been recorded for *An. studiosus* (Furey 1998; Duncan et al. 2010) and *Theridion grallator* (Gillespie 1990), *Scytodes pallida* (Li & Kuan 2006), as well *St. tentoriicola* (Ruch et al. 2009b). Thus, limited dispersal and some inbreeding in subsocial

ancestors may have purged deleterious alleles from the population and lessened the cost of inbreeding.

Increased competition is one of the automatic costs of any social group (Alexander 1974), and food resources may determine whether social groups can persist or not. It has been shown that supplementing prey can extend the gregarious phase in *Coelotes terrestris* (Krafft et al. 1986), *Theridion pictum* (Ruttan 1990), and *Amaurobius ferox* (Kim 2000). Smaller spiders tend to disperse sooner in *Scytodes pallida* (Li & Kuan 2006) *Am. ferox* (Kim 2000) and *Th. pictum* (Ruttan 1990), and spiders from larger colonies also disperse sooner in *Sc. pallida* (Li & Kuan 2006). The dispersal patterns of *Anelosimus arizona* are consistent with escape from resource competition, rather than mate competition or inbreeding (Powers & Avilés 2003). These studies suggest that prey limitation may be the ultimate cause for dispersal from the natal nest. It has been argued for the genus *Anelosimus* that the cooperative prey capture of large insects, by making new food resources accessible, overcomes food limitations, and the distribution of social species tracks with the abundance of large prey items (Avilés et al 2007; Powers & Avilés 2007; Yip et al. 2008).

There is evidence for one reversion to a less social state in the genus *Anelosimus*. *Anelosimus pacificus* and its related species have a very short duration of maternal care, and their web structure is more similar to webs of solitary theridiids than other *Anelosimus* (Agnarsson et al. 2006b). Other species that are either solitary or have very short periods of maternal care have also been described from Madagascar, and interestingly, the closest relatives of these spiders are *A. pacificus* and its relatives in South America, although others of this clade will likely be found in Africa (Agnarsson

et al. 2009). This clade is nested within the more social *Anelosimus*, suggesting a reversion to a less social state (Agnarsson et al. 2006b). Other reversions are possible, but at this time, phylogenetic analyses on social behavior are only available for *Anelosimus* (Agnarsson et al. 2006a, 2006b) and *Stegodyphus* (Kraus & Krause 1988; Johannesen et al. 2007).

Without phylogenetic analyses on more subsocial taxa, we cannot say whether reversions to less social states are common or rare. However, one consequence of subsociality is the evolution of altriciality, which may block the evolution to less social states. Once juveniles secure most of their nutrition from their mother, it may be more advantageous to allocate resources away from structures necessary for prey capture. For example, *Amaurobius ferox* spiderlings lack sclerotized chelicerae and a functional cribellum, the structure required to spin sticky silk, and cannot feed on their own until the third instar (Kim 2000). Similarly, in *Anelosimus studiosus*, spiders cannot feed themselves until the third instar and die of starvation if the mother does not feed them by regurgitation (Brach 1977). Once juveniles evolve altricial development, any decrease in maternal care would likely have dire consequences for maternal fitness and be selected against.

Transitional species

It is clear that categories of sociality are artificial, if useful, delineations imposed on what is actually a continuum of behaviors (Agnarsson 2006), and several species share characteristics of different levels of sociality. The crab spiders *Diaea megagyna* and *Di. socialis* both mate within the natal nest and display female biased sex ratios typical of

cooperative social species (Avilés 1997). These species have overcome the cost of inbreeding, yet dispersal is still less costly than attempting to reproduce within the group. Some individuals of both *Anelosimus studiosus* and *An. jabaquara* remain in their natal nest to mate and raise their offspring. *An. jabaquara* females aggressively defend their egg sacs from other females in the group, but after fourth instar, broods of different females within the colony mix and cooperate (Marques et al. 1998). In populations of *An. studiosus* in Tennessee, the average number of adult females per nest is 3.7 (Furey 1998), and there appears to be a consistent dichotomy between social and asocial individuals (Furey 1998; Pruitt et al. 2008). Interestingly, *An. studiosus* lives much farther north than any other permanent social species, defying the general pattern that social *Anelosimus* are restricted to the lowland tropics (Avilés et al. 2007). *An. studiosus* adult females are, paradoxically, more likely to live in social groups in colder climates, and Jones et al. (2007) argued that this is because females are more likely to die in colder climates and having foster mothers in the same nest guards against total brood failure.

It is also clear that there are several species that have very short periods of association, usually just one or two instars, and are thus similar to transient subsocial species (Table 1). In *Cheiracanthium japonicum*, for example, the mother provides only one meal to her offspring by matriphagy, and the offspring soon disperse (Toyama 2001). It is less clear how many cases of maternal care and subsociality are facultative. Orphaned spiderlings are sometimes observed (e.g. Gillespie 1990), but it is usually impossible to determine whether the mother abandoned the nest to reproduce elsewhere or died. Scytodid mothers sometimes abandoned their offspring to build a

separate web in the laboratory (Li et al. 1999). Adult *Delena cancerides* females were observed to abandoned their offspring in the field (which did not follow them), but only if their bark retreat was disturbed (Yip & Rayor 2011). The lycosid, *Geolycosa turricola*, is facultatively subsocial in that only a third to a half of spiderlings remain in the natal burrow while the rest disperse prior to feeding (Miller 1989). The fact that juveniles, and not the mother, control the termination of maternal care, suggests that maternal care or remaining in the natal burrow entails costs as well as benefits to spiderlings, but what those costs might be has not been investigated.

Conclusions and outlook

Many thousands of spider species display transient subsocial behavior and care for young juveniles, yet only a tiny fraction continue to interact after the juveniles begin to feed. The barriers to prolonged subsocial behavior are therefore considerable. These barriers are the cost to the mother in terms of lost fecundity, competition with siblings for resources, and the threat of filial cannibalism. Despite the barriers, subsociality has arisen many times with a great diversity of duration, mode of provisioning, communication, and cooperation.

Throughout this review we have highlighted profitable areas of future research. Much research on subsocial behavior in spiders has focused on simple descriptions of behavior. Obviously, we believe reporting this fundamental biology must continue as subsocial behavior is described for more and more species. However, certain areas are in need of manipulative experiments, especially in the field. So much of our understanding of the fitness consequences of subsocial behavior rests on interactions

with predators and prey, the full diversity of which cannot be replicated in the laboratory. In particular, we know very little about predation, the effectiveness of maternal defense, the role siblings play in predation risk, and the survival cost of maternal care. We also lack data on prey capture in the field, the importance of maternal provisioning relative to prey capture by juveniles, the role of sibling cooperation, and impact of cheaters that feed without participating in prey capture. Field observations are undoubtedly difficult but nonetheless possible. Several studies have cataloged natural prey capture (Powers & Avilés 2007; Jones & Parker 2002; Yip et al. 2008; Yip & Rayor 2011), and artificial 'nest boxes' for spiders can help circumvent the secretive habits of some species (Yip & Rayor 2011). We also have little understanding of communication within groups. The role of vibratory and chemical cues in regulating feeding, aggression, and escape behaviors is still largely unknown. Finally, there are virtually no studies comparing the ecology of subsocial spiders and their transient subsocial relatives. Comparative studies will help to tease apart the potential forces behind the evolution of subsociality: prey abundance, predation pressure, semelparity, nest structure, female promiscuity, and others. These studied must be accompanied by phylogenetic analyses, testing the sequence of traits in evolutionary time and allowing us to separate cause from consequence.

We began this review by asserting that sociality was particularly rare in spiders. Certainly this is the case if we compare the 60 subsocial species listed here to the many thousands of species displaying advanced parental care in the birds alone, for example. However, the spiders have independently evolved subsociality at least 18 times. Because our definition of subsociality is specific to the spiders, it is difficult to compare

numbers directly to other taxa. For example, parental care of any kind is known in 89 families of fishes (Blumer 1982), but this includes nest construction and egg guarding, which we explicitly excluded from our review on spiders. However, we can draw interesting comparisons of parental provisioning behavior. Parental feeding of fry is known in two families of fish (Blumer 1982; Clutton-Brock 1991; Wisenden et al. 1995). Parental feeding of the offspring is known in only two families and three genera in amphibians (Crump 1996), and parental care arose only once each in the ancestors of the birds and mammals (Farmer 2000; Burley & Johnson 2002). Therefore, while very few spider species are subsocial, it is likely that parental feeding of the offspring evolved more times in the spiders than in all vertebrates combined. The repeated evolution of subsociality in the spiders provides many natural replicates with which to help answer why parents extend care beyond the egg and, further, beyond the age at which offspring could be independent. It is still poorly understood why some species evolve sociality while other do not (Tallamy & Brown 1999; Hatchwell 2009), and the extension of maternal and sibling bonds are a key step toward more complex societies in the spiders and other organisms. Further investigation into the spiders will provide insight into the evolution maternal care, subsociality, and a diversity of other societies.

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Table 1

	Family	Genus	Species	Duration of Association (time/instar)	Sib Coop?	Persists Beyond Mother?	Provisioning Type	Clutch Size: mean (range)	Number of Clutches	Nest Type	Location/Habitat	References
Mygalomorphs	Dipluridae	*Ischnothele*	*caudate*	17+ wks	?	n	P	300	1-4	Funnel + sheet	Yucatan, Mexico. to northern S. America; palm trees/litter	Jantschke & Nentwig 2001
		Heterothele	*darcheni* = *Macrothele darcheni*	Penultimate or ultimate instar	?	y	?	?	?	Funnel + sheet	Rainforest, Gabon	Darchen 1967
	Nemisiidae	*Nemesia*	*caementaria*	3-5 yrs/6-10th instar	?	n	P	40	?	Burrow	Mediterranean basin, near walls	Buchli 1969
	Theraphosidae	*Hysterocrates*	*crassipes*	?	?	?	P	?	?	?	Cameroon	Varrecchia et al. 2004
			gigas	3+ mo	y	?	P	? (14-49)	?	Burrow	Rainforest and grasslands of Nigeria, Cameroon, Congo	Varrecchia et al. 2004
		Poecilotheria	*regalis*	?	n	?	None	?	?	Sheet on bark	India	L.S. Rayor pers. obs.
		Xenesthis	*immanis*	?	?	?	P	?	?	Burrow	Rainforest, Peru	Cocroft & Hambler 1989
Araneomorphs	Agelenidae	*Coelotes*	*terrestris*	5-6 wks		n	P, E, (M)	60 (40-80)	1	Sheet + funnel + burrow	European woodlands	Gunderman et al. 1991,1997; Krafft et al. 1986
		Tegenaria	*atrica*	4 wks/4th - 5th instar	n	n	P	80	2	Sheet + funnel	Central Europe	Trabalon et al. 1996
	Amaurobiidae	*Amaurobius*	*fenestralis*	4 wks	y	y	E, M	39	1	Sheet + retreat	Europe, rock crevices	Bristowe 1971; Tahiri et al. 1989
			ferox	4-5 wks	y	y	E, M	80 (40-135)	1	Sheet + retreat	Europe, shaded and damp areas	Bristowe 1971; Kim and Krafft 2005
			similis	?	?	?	?	50	?	Sheet + retreat	Europe	Kaston 1965; Bristowe 1971

Desidae	*Phryganoporus*	*candidus*	1 yr/ antepenultimate or penultimate	y	y	P	26.9	1 to 16 mean 6.4	Sheet + funnel	Dry tropical sclerophyll forest; Townsville Queensland	Downes 1992/1993
		= *Ixeuticus candidus; Amaurobius socialis; Phryganoporus gausapata; Badumna candida*									
Eresidae	*Eresus*	*cinnaberinus*	6th instar	y	y	R, M	60	1	Silk lined burrow	Widespread in Europe; dry steppe habitat	Kullmann & Zimmermann 1974; Johannesen et al. 1998
		= *E. niger*									
	Stegodyphus	*lineatus*	30-50 days/ultimate (Male)	y	y	R, M	46 (0-113) or 90 (Schneider 1995) or 120 Kullmann 1972	1	Silk tube + capture web	Entire Mediterranean region	Schneider 2002; Lubin & Ward 1993
		pacificus	5th instar	y	y	R, M	450	1	?	Jordan to India	Kullmann 1972
		tentoriicola	Possibly to adult	y	y	R, M	?	1	?	Cradock South Africa; acacia grassland	Ruch et al. 2009 a,b
Filistatidae	*Kukulkania*	*geophilis*	1-2 wks	y	?	?	?	?	Crevice + radiating web	Los Angeles, California	Cokendolpher & MacDonald 2008
		hibernalis	8 wks/3rd instar	y	n	P	81	1 at a time	Crevice + radiating web	SE USA	Curtis & Carrel 1999
Lycosidae	*Aglaoctenus*	*lagotis*	3 days	n	n	R	?	?	Sheet + funnel	Argentina to Brazil	Stefani et al. 2011
	Geolycosa	*turricola*	40+ days, maybe up to a few months?	y	n	P	?	1	Burrow	Red cedar scrub	Miller 1989
	Sosippus	*floridanus*	5 mo	?	n	P	20-70	1	Sheet + funnel	Open sandy areas and palmetto, Florida	Brach 1976
		janus	2-4 instars	?	?	P	?	?	Sheet + funnel	Mesic habitat, Live Oak woodland, Florida	Brady 2007
Miturgidae	*Cheiracanthium*	*japonicum*	2 wks	n	n	M	100	1	Rolled leaf	Grassland, Hokkaido Japan	Toyama 2001, 2003
Salticidae	*Menemerus*	*bracteatus*	4-6 instar	?	?	?	23.8 (9-45)	1-4	Silk	Eucalyptus forest	Rienks 2000

								(mean 2)	enclosure under bark	near Brisbane Australia	
Scytodidae	*Scytodes*	*fusca*	3rd instar	n	n	P	?	1, rarely 2?	Sheet + funnel	Rainforest tree trunks Cairns Australia	Bowden & Jackson 1988; Bowden 1991
		intricata	3-4th instar	y	y	None	?	1	3D heet + funnel	Costa Rica, Panama	Eberhard 1986
		Pallida	7-22 days/2nd-4th instar	y	y	P	21	1, rarely 2?	Silked up leaves	Singapore botanic gardens	Yap & Li 2009; Li & Kuan 2006; Li 2002
		Sp	15 days/3rd instar	y	y	P	?	1	Sheet + funnel	Tropical rain forest, Philippines	Li et al. 1999
Sparassidae	*Delena*	*cancerides*	1 year/ultimate or penultimate	y	y	P	(40-80)	1 to 5	Silk enclosure under bark	Much of southern Australia	Rowell & Avilés 1995; Rayor et al. in prep.
Theridiidae	*Achaearanea*	*kaindi*	?	?	?	P	?	?	?	Montane forests of Papua New Guinea	Lubin 1982
		riparia	1 mo	y	?	P	?	1 or 2	3D mesh + cone retreat	Europe and Russia	Norgaard 1956
		= Theridion saxatile									
		mundula	?	?	?	P	?	?	3D sheet	Cali Columbia, dry tropical forest	Eberhard 1972
		=A. tesselata									
	Anelosimus	*analyticus*	?	y	?	?	?	?	?	Venezuela to southwest US	Agnarsson 2006; Stejskal 1976
		andasibe	?	?	?	?	?	?	3D sheet	Montane rain forests of Eastern Madegascar	Agnarsson & Kuntner 2005
		arizona	9 mo/ 5-7 instar	y	y	? (M)	35.4 (21-53)	1	3D sheet	Semi-arid riparian; SE Arizona, USA	Avilés & Gelsey 1998
		crassipes	2 wks; 1 or 2 instars	n	n	P	40 (28-51)	1	3D mesh	Ninomiya Japan, seashores	Ito & Shinkai 1993
		elegans	?	?	?	?	?	?	3D sheet	Cloud forest Ecuador	Agnarsson 2006
		jabaquara	11-12 mo; subadult or never	y	y	P, R	49.4 (18-76) singles; 20.7 (15-31)	1	3D sheet	Sao Paulo, Brazil, forest edge and interior	Marques et al 1998; Gonzaga &

						groups				Vascolcellos-Neto 2001
	*jucundus (baeza?)***	10-11 mo/ ultimate or penultimate	y	y	?	?	2 or 3	3D sheet	Wet tropical and pre-montane forest; Mexico to Peru; Tena, Ecuador	Nentwig & Christenson 1986; Agnarsson 2006; Avilés et al. 2001; Powers & Avilés 2007
	kohi	To near adulthood	?	?	?	?	2+?	3D sheet	Malaysia and Singapore, near the beach	Agnarsson & Zhang 2006
	may	?	?	?	?	?	?	3D sheet	Montane rain forests of eastern Madagascar	Agnarsson & Kuntner 2005
	nazariani	At least to antepenultimate	?	y	?	?	?	3D sheet	Montane rain forests of eastern Madagascar	Agnarsson & Kuntner 2005
	pacificus	1 or 2 instars	n	n	P	26 (from one egg sac)	1 (maybe others after AF abandons juvs)	3D mesh	Costa Rica, on *Ficus* trees along the beach	Agnarsson et al. 2006
	sallee	?	?	?	?	?	?	3D sheet	Montane rain forests of eastern Madagascar	Agnarsson & Kuntner 2005
	*studiosus**	1 yr, or never	y	y	P, R	32 (0-74)	1	3D sheet	South US to Rio de la Plata (39' N to 33' S)*	Viera et al. 2007; Brach 1977
	vondrona	?	?	?	?	?	?	3D sheet	Montane rain forests of eastern Madagascar	Agnarsson & Kuntner 2005
Argyrodes	*flavipes*	10 days, 1 molt	y	n	P, R	20	1 or 2	3D mesh (under leaf)	Australian rain forest	Whitehouse & Jackson 1998
Chrysso	*nigricepts*	?	?	?	?	?	?	?	Columbia to Ecuador	Miller & Agnarsson 2005
Helvibis	*theorelli*	Ultimate or penultimate	y	?	P	20 (14-24)	1	3D mesh (under leaf)	Commune Regina, French Guiana; lowland rainforest	Coddington & Agnarsson 2006
Latrodectus	*species*	Penultimate at least	y	?	P	?	1	3D mesh	Serra do Cipo National Park Brazil.	Bertani et al. 2008
Theridion	*grallator*	40-100 days/3-4th instar	n	n	P	43.8 (14-70)	1	3D mesh (under leaf)	Wet and mesic forests of Hawaii	Gillespie 1990
	impressum	1 instar	n	n	P, R, M	100 (48-156)	1	3D mesh	Much of Europe, including agricultural fields	Kullmann 1972; Kullmann &

											Zimmermann 1974; Pekár 2000
		japonicum	1 mo	?	n	P, M	20	3-8 but only two eclosed	?	Widely distributed in Japan	Ito 1985
		pictum	32 days	n	n	P	60	2	3D mesh	Northern Minnesota	Ruttan 1990
		sisyphium	5th instar	y	y	P, R	50	1	3D mesh	Europe (Holarctic)	Kullmann 1972; Kullmann & Zimmermann 1974
		= T. notatum									
Thomisidae	*Diaea*	*ergandros*	1 yr/adults	y	y	E, M	45 (15-80)	1	Leaves bound by silk	Closed canopy *Eucalyptus* forests of Australia; Tasmania to S. Queensland	Evans 1995; Evans 1998
		megagyna	1 yr	y	y	?	?	1	Leaves bound by silk	Closed canopy *Eucalyptus* forests of Australia; NSW to S Queensland	Evans 1995
		socialis	18 mo	y	y	P, M?	?	1	Leaves bound by silk	Closed canopy *Eucalyptus* forests of southern Australia	Main 1988; Evans & Main 1993
Uloboridae	*Philoponella*	*congregabilis*	?	y	?	P, R	?	?	Orb + 3D mesh	Dry schlerophyll woodland Australia	Clyde 1969; Downes 1995
		= Uloborus congregabilis									

Table 1

Summary of the biology of all known subsocial spiders. Provisioning types are defined as P = prey sharing/dropped prey; R = regurgitation; E = trophic eggs; M = obligate matriphagy; (M) = facultative matriphagy. * Note that *An. studiosus* is probably a complex of several species (Agnarsson 2006). ** It is unclear whether any studies have examined *An. jucundus* or whether they have studied *A. baeza* (Agnarsson 2006).

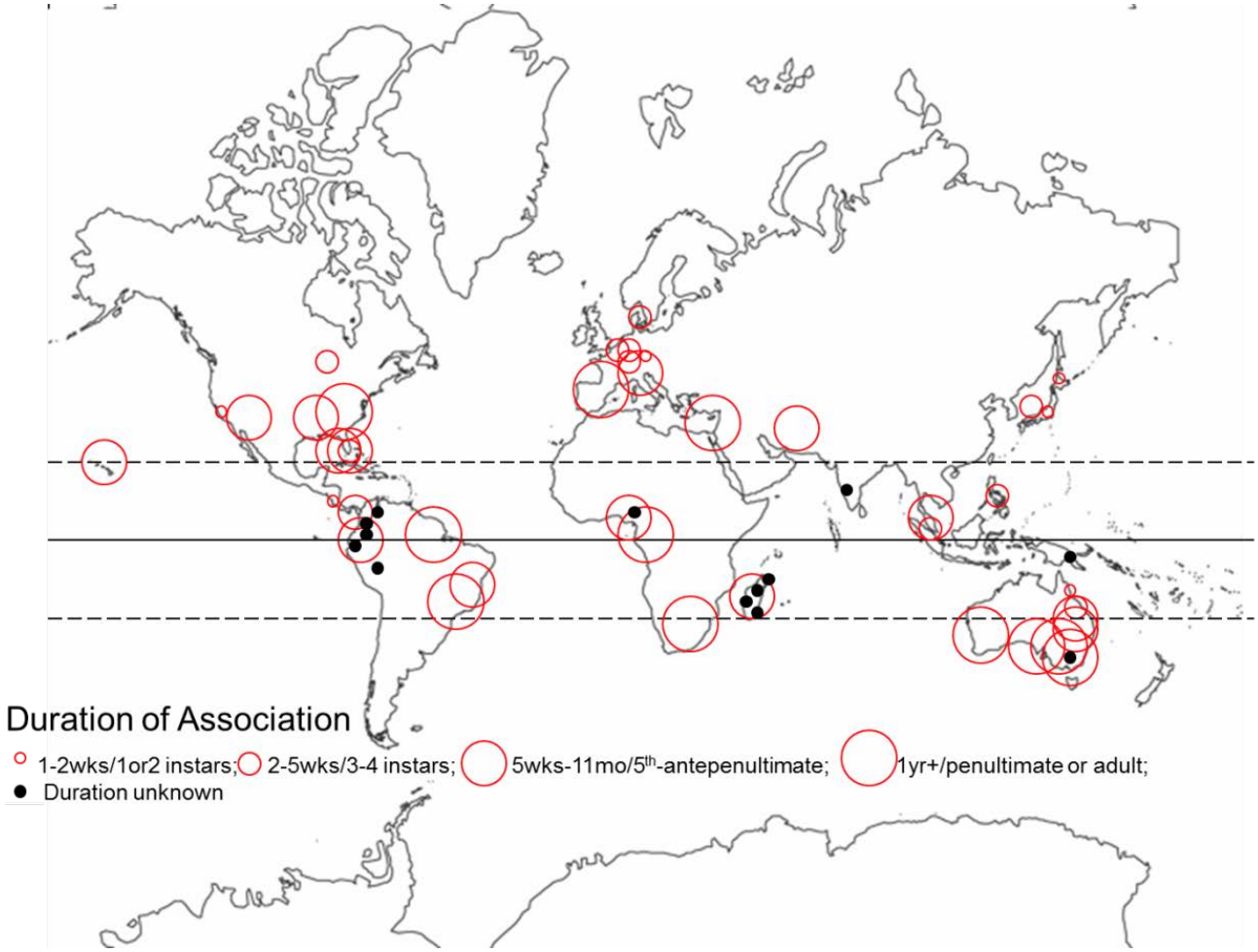

Figure 1. The geographic distribution of subsocial spiders. Circle size indicates the duration of association. Filled dots indicate species for which the duration is unknown. The solid horizontal line indicates the Equator, and the dashed lines indicate the Tropics of Cancer and Capricorn.